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Influence of weather on movements and migrations of caribou

Eastland, Warren George, Ph.D.

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U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

INFLUENCE OF WEATHER ON MOVEMENTS AND MIGRATIONS OF CARIBOU

A

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Warren G. Eastland, B.S., M.S.

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INFLUENCE OF WEATHER ON MOVEMENTS AND MIGRATIONS OF CARIBOU

By

Warren G. Eastland

RECOMMENDED:

Advisory Committee Chair

Advisory Committee Chair

Department Head

APPROVED:

Dean, College of Natural Sciences

Dean of the Graduate School

5/1/91
Date

ABSTRACT

Caribou (Rangifer tarandus granti) are typified by use of calving grounds and by making twice-annual migrations between summer and winter ranges. This study used satellite technology to examine the influence of weather on calving site selection, autumn and spring movements, and timing and directionality of migrations of the Porcupine Caribou Herd (PCH) that calves in northeast Alaska and northwestern Canada adjacent to the Beaufort Sea. The reigning hypothesis that females select areas that become free of snow early for calving sites was rejected because females selected areas of >75% snowcover ($P = 0.02$) preferentially for calving. Benefits from use of mottled snow for calving were access to vegetation in its early phenological stages and protection for their calves from predators. Access to nutritious forage and predator avoidance appeared to be the main reasons for calving site selection.

Multiple linear regression models were used to examine rate and direction of autumn and spring migrations using weather data from U.S. and Canadian sources. Weather was found to be both an ultimate and an approximate influence on the rate and direction of autumn migration ($P < 0.05$). Explanatory power of the equations was low ($R_a^2 < 0.41$). Proximal causes of movement were best explained by caribou tracking of vegetation phenology. Pre-rut movements in September lacked concurrence between rate and direction whereas rate and direction were related in October.

Models of spring migration of parturient females indicated a common timing among years, late April and early May, and movements were significantly affected by weather ($P < 0.02$), in particular snow depths and conditions that would affect foraging and traveling conditions. This study suggests that: 1) females preferentially use areas of delayed snow melt for calving, and 2) weather influences both spring and autumn migration of caribou, although the effect of weather may be more indirect than direct.

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BACKGROUND

Animals inhabiting environments with seasonal extremes adapt primarily by avoiding the extremes (i.e., hibernation and estivation), by occupying habitats less subject to extremes (i.e., rivers and lakes), or by using different habitats during seasonal extremes (i.e., migration) (Kendeigh 1961, Levins 1968, Fretwell 1972). Migration by populations of large herbivores may be selected for not only as a response to changes in abundance and quality of forage but also as a mechanism whereby individuals reduce their risk of predation (Fryxell and Sinclair 1988). Levins (1968) suggested that an alternative to avoiding seasonal extremes in habitat condition would be for animals to adapt to conditions and habitats intermediate between the extremes and avoid costs associated with migration. Although this hypothesis deals with large scale migrations that result in major latitudinal changes, it has application to migrations of a smaller scale. Local adaptation to avoid migrating would decrease the total amount of habitat available. From an ecological perspective the overall carrying capacity of an area might be lessened.

Migrant populations, then, should outnumber resident ones in areas subjected to similar predation pressures and changes in forage availability and quality because of more efficient use of resources by migrant populations. This appears to be the case for barren-ground caribou (Rangifer tarandus granti) in arctic Alaska. Highly migratory populations of caribou, such as the Porcupine Caribou Herd (PCH) (Fig. 1) and the Western Arctic Herd, outnumber the more sedentary Central Arctic and Teshekpuk herds. The preceding comments assume that larger population size results from increased ranges available to the highly migratory herds. This study does not address the issue of why some herds migrate and others do not, but extensive migrations may be the result, rather than the cause, of increased population size.

This study addresses correlates of migration for the PCH, which has

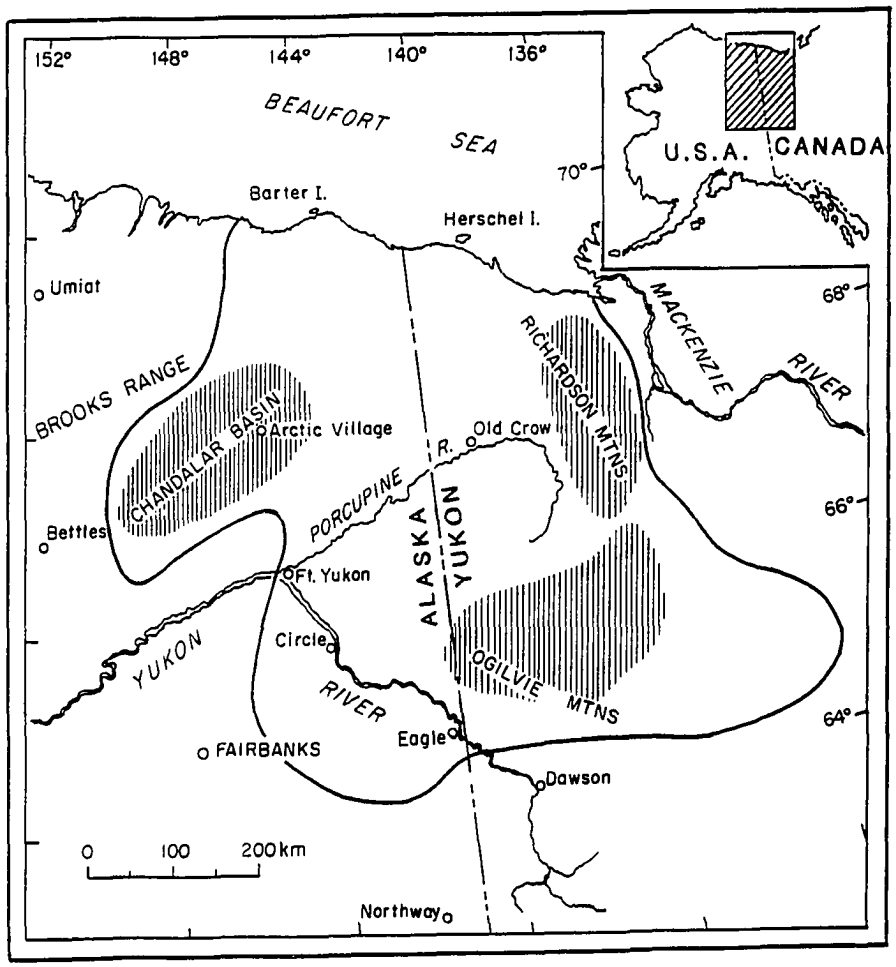

Figure 1. Total range of the Porcupine Caribou Herd.

a well-known migration pattern (Skoog 1968, Jakimchuk et al. 1974, Roseneau et al. 1975, Surrendi and DeBock 1976, Thompson 1978, Ealey 1980, Whitten and Cameron 1983, Garner and Reynolds 1986) and has been the subject of considerable research because of potential oil exploration and development on its calving grounds in the Arctic National Wildlife Refuge (Clough et al. 1987, Sheldon 1988).

A caribou herd is defined as a group of caribou that consistently calve in a location distinct from calving areas used by other herds (Skoog 1968). The PCH numbered about 178,000 animals in 1989 (Whitten and Fancy 1990), and is the second largest of the Alaskan herds. The historic range of the PCH extends from between 137° and 146° west longitude along the Beaufort Sea and south to Dawson in the east and the Tanana Hills in the west (Fig. 1). The herd migrates from the calving grounds and roughly adjacent summering areas to the wintering areas in the autumn and return in the spring; yearly distance traveled may exceed 5000 km (Fancy et al. 1989).

Calving grounds of the PCH are located on the arctic coastal plain north of the Brooks Range from the Babbage and Blow Rivers in Yukon Territory west to the Canning River in Alaska. PCH females calve in late May and early June (Garner and Reynolds 1986, Eastland and White 1990). Selection of specific sites within the overall calving grounds has been attributed both to snow conditions that allow females early access to forage (Lent 1980, Eastland et al. 1989) and predator avoidance (Bergerud and Page 1987; Fancy and Whitten, in press). Females of the PCH rear their calves on the coastal plain or in adjacent foothills of the Brooks Range during June and early July (Jakimchuk et al. 1974, Roseneau et al. 1975, Surrendi and DeBock 1976). In late July and August, the herd shows a strong tendency to disperse with some animals remaining on the coastal plain and others moving south of the Brooks Range into both Alaska and the northern Yukon Territory, Canada (Roseneau et al. 1975, Surrendi and DeBock 1976, Thompson 1978, Ealey 1980). During autumn the herd

aggregates into bands and a slow migration generally is thought to begin in September and end between late October and December (Jakimchuk et al. 1974, Roseneau et al. 1975, Surrendi and DeBock 1976, Thompson 1978, Ealey 1980, Whitten and Cameron 1983). October is also the period of rutting activity, ending as the herd splits or disperses to its wintering areas.

Habitat choice for an animal in a changing environment is a function of the time and energy necessary to search out that habitat and the probability that search efforts will enhance fitness of the searching organism (Levins 1968). Individuals of a population exposed to regular changes in resource quality and abundance must redistribute themselves prior to the period of resource restriction for optimal habitat use (Geist 1971, Fretwell 1972, Alcock 1984).

The seasonal light regime has been suggested as the "timer" for migration (Skoog 1968, Geist 1971, Pendergast 1973, Bergerud 1974). Daylength, mediated through the pineal gland, regulates melatonin production, which in turn influences timing of mating (Adam and Atkinson 1984, Ryg 1986) and may therefore influence timing of autumn migration.

In contrast, autumn migration of the PCH generally has been attributed to a response to weather (Banfield 1954a, 1954b; Kelsall 1968; Jakimchuk et al. 1974; McCourt et al. 1974; Surrendi and DeBock 1976; Thompson 1978, Ealey 1980), although Pendergast (1973) speculated there was an intrinsic predisposition to autumn migration. Conversely, timing of spring migration by parturient females has been thought to be primarily a response to intrinsic factors associated with pregnancy, but proximally mediated by snow conditions that impede movement in some years (Skoog 1968, Bergerud 1974, Thompson 1978). Females, driven by the need to reach the calving grounds prior to parturition, are thought to be held back from early migration by snow or other weather conditions that make the energetic cost of traveling and foraging too expensive.

These generalities, observations and hypotheses addressing caribou movements have been based on incidental observations of unmarked caribou,

and in later years by VHF radio-tracking (Banfield 1954a, 1954b; Kelsall 1968; Skoog 1968, Jakimchuk et al. 1974; McCourt et al. 1974; Surrendi and DeBock 1976; Thompson 1978, Whitten and Cameron 1983, Ealey 1980). The latter radio-tracking studies have been hampered by the darkness and extreme weather conditions inherent in Arctic and Subarctic latitudes such that continuous monitoring of focal animals as a means of documenting movements in relation to light, weather, and other factors has not been attempted.

Advances in satellite imagery (LaPerriere 1976) and telemetry (Curatolo 1986, Fancy et al. 1988) have refined techniques for studying caribou location and movements. When combined with weather data and ground observations of vegetation use, they lead to advances in understanding of caribou ecology by providing data in greater amount and detail than previous methods could provide.

In this study, I used multiple linear regression, a commonly used statistical technique for examining ungulate ecology (Bartmann and Bowden 1984, Wehausen et al. 1987, Beier and McCullough 1990) to couple satellite imagery and tracking of caribou with weather data gathered by U.S. and Canadian weather services to resolve inconsistencies present in literature about calving site selection by caribou, and the influence of weather on caribou spring and autumn migrations. Satellite imagery was extracted from archived images at the University of Alaska Fairbanks and satellite telemetry data for caribou movements was provided by the Alaska Fish and Wildlife Research Center, U.S. Fish and Wildlife Service, Fairbanks.

The objectives were:

1. To determine the influence of snowcover on the selection of calving sites by females of the Porcupine Caribou Herd.
2. To examine the hypothesis that weather is the primary influence on autumn migration of the Porcupine Caribou Herd.
3. To examine the degree to which weather affects the spring migration of females of the Porcupine Caribou Herd.

CALVING SITE SELECTION

INTRODUCTION

Proposed development of portions of the Arctic National Wildlife Refuge has implications for PCH calving success and recruitment (Clough et al. 1987). The proposed development establishes the need to understand ecological relationships of the coastal plain with respect to its role as a calving ground and for early post-natal nutrition of barren-ground caribou.

Snowcover has been considered an important factor in selection of calving sites by reindeer and caribou (Kelsall 1968, Skoog 1968, Thomson 1977, Lent 1980, Fleck and Gunn 1982, Bergerud and Page 1987). Nevertheless, previous studies of the relation of snowcover and selection of calving sites by barren-ground caribou within traditional calving areas have yielded conflicting results. Although many reports implicate snow-melt as a factor in selection of specific calving grounds by caribou, quantitative data are lacking.

Specific sites used by the PCH for calving have varied among years (Garner and Reynolds 1986). Selection of an area for concentrated calving activity within the general calving grounds in any particular year appears to depend on the interaction of weather patterns that facilitate caribou access during spring migration (Roseneau and Curatolo 1976; Surrendi and DeBock 1976; Garner and Reynolds 1986; Fancy and Whitten, in press) and the degree of snow-melt on the calving grounds (Kelsall 1968, Skoog 1968, Lent 1980).

Areas of substantial snowcover are thought by some to be avoided by parturient caribou. Lent (1980) reported positive correlations between specific calving zones of the PCH and snow-free areas using LANDSAT

imagery. However, he based his conclusions on 1972-73 calving data and information on snowcover from 1978. Conversely, Fleck and Gunn (1982) reported that calving grounds for the Bathurst, Beverly, and Kaminuriak herds in Canada were those areas where snow persisted the longest.

I reexamined the relationship between published reports of caribou calving locations and snowcover from satellite imagery over a 10-year period between 1974 to 1987 for Porcupine Caribou calving on the arctic coastal plain. I tested for differences in selection of 3 snowcover categories by females, and developed a statistical model to predict the amount of snowcovered area contained within the concentrated calving area.

STUDY AREA

Calving grounds of the PCH extend across the arctic coastal plain (68° to 70° N lat.) of NW Canada and NE Alaska from approximately 137° to 146° west longitude, a distance of ca. 350 km. Elevations extend from sea level to about 600 m in the foothills of the Brooks Range.

Predominant vegetation is tundra and low-growing shrubs with some taller Salix spp. growing along the braided, low-gradient rivers. Other genera include Arctagrostis, Betula, Carex, Dryas, Eriophorum, Equisetum, Lupinus, Saxifraga, and others. Plant nomenclature follows Hultén (1968). Calving grounds in Alaska are within the Arctic National Wildlife Refuge, described more fully in Garner and Reynolds (1986).

METHODS

Snowcover

Snowcover data for 1974 to 1987 was extracted primarily from Tiros-N satellite imagery (1:5,000,000 scale) archived at the Geophysical Institute, University of Alaska Fairbanks. Snowcover was assigned to one of three categories: 1) >75% snowcover; 2) 25-75% snowcover; and 3) <25% snowcover. Other satellite imagery (LANDSAT and Defense Meteorologic Satellite Program) was available for a limited number of days and was used to supplement Tiros-N imagery. Additional observations were made from

aircraft and the ground, but it was not possible to map snowcover over this vast area during the brief calving season.

On a 1:1,000,000 map of the calving area, I defined 20 ground-units ($\bar{x}$ = 790 km^2, SD = 421 km^2, range = 258 - 2002 km^2) (Fig. 2) using distinct geographical features visible on Tiros-N satellite photographs and categorized snowcover for each ground-unit. Major rivers, including the Canning, Sadlerochit, Jago, Aichilik, Kongakut, Firth, and Babbage were used as east-west boundaries of the units; north-south boundaries were defined by elevational gradients.

Information on snowcover was compared with maps of concentrated calving areas ($\bar{X}$ = 2090 km^2, SD = 836 km^2, range = 381 - 3345 km^2) that were derived from data gathered about 5 June of each year (Garner and Reynolds 1986:215-228; USFWS unpubl. data). Snowcover and concentrated calving sites were compared for 1 June each year because pregnant cows usually arrived at their intended sites of calving during the last days of May or early June; these females remain near their calving sites for 7-10 days (K. R. Whitten, AK Fish and Game Dep., pers. comm.) Thus, snow conditions prevalent on about 1 June were those encountered by most females when they selected sites for calving. Clouds obscured some ground-units on 1 June in some years, so occasional interpolation of snowcover from adjacent days was required.

Maps of concentrated calving areas were overlaid on the ground-unit map and the proportional amount of each snow category was determined for each unit. Availability was calculated as the proportion of each snowcover category on the coastal plain as far west as calving was confirmed to have occurred in a particular year. This was done because parturient females of the PCH first arrive on the eastern portion of the coastal plain and move in a westerly direction, and a bias would be introduced if the entire western portion of the calving grounds were considered available for calving every year. An index for each snowcover category was calculated comparing use to availability [(use /

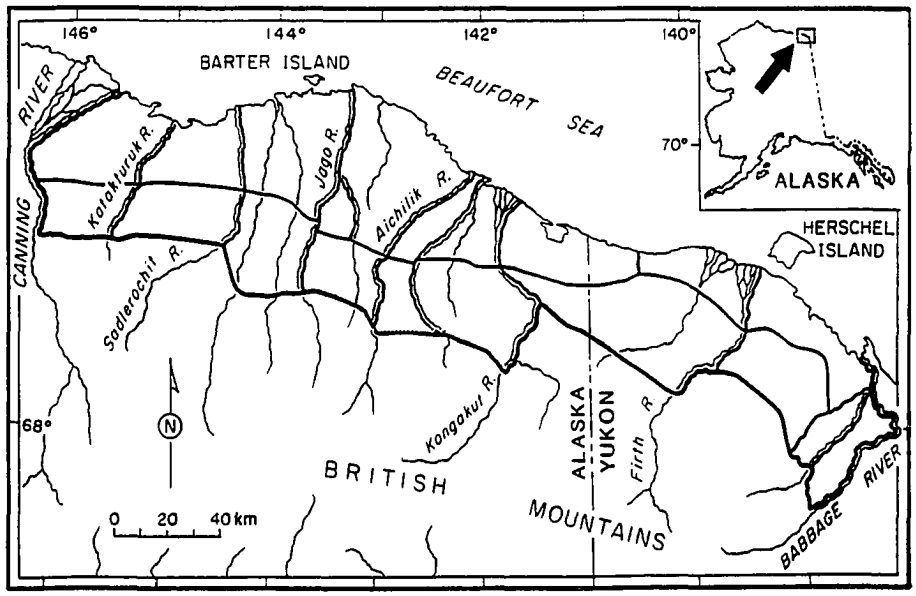

Figure 2. Location of ground-units used for classifying snowcover on the calving grounds of the Porcupine Caribou Herd in northeast Alaska and western Canada, 1974 - 1987.

availability) - 1]. Use was considered to be the proportion of each snow category within each year's concentrated calving area. Availability was the proportion of each snowcover category on the coastal plain used by caribou for more scattered calving activity plus the areas of concentrated calving. Negative values of the index indicated coverage of a snow category within the concentrated calving area was less than that snow category's proportional coverage of the available calving area; positive values indicated coverage to a greater degree; and values of zero indicated equivalent proportions. The G-test of independence (Zar 1984: 52-53) was used to test for differences between snowcover use and availability among number of years.

Proportion of snowcover in the concentrated calving area (Y) was regressed against weather variables (X_i). Weather data from Barter Island (Natl. Oceanic and Atmos. Adm., Natl. Climatic Data Cent., Asheville, NC) were selected for alternate days from 22 May through 5 June. Absolute values for climatic variables may differ between Barter Island and the calving grounds. I believe, however, that weather data from Barter Island provided reliable indices to weather on the arctic coastal plain, where there were no permanent weather stations. Among the climatic variables I considered for inclusion in the model were daily values for minimum temperature, maximum temperature, average temperature, snow on ground, snow fall, average wind vector, average wind speed, greatest wind speed, average cloud cover, and derived variables (e.g., average daily temperature change, difference between wind vector and wind speed), and others.

Variables considered for the model were examined for linearity and normality (Snedecor and Cochran 1980: 78-81); those violating assumptions for regression analysis were transformed (Snedecor and Cochran 1980:288-292). A Pearson correlation matrix was used as an informal test for independence of weather variables (X_i). No variables with an absolute value of $r \geq 0.7$ were allowed to enter the regression model concurrently.

Additional formal testing for multicollinearity, including examination of variance inflation factors and partial coefficients of regression, was completed after the model was built (Neter et al. 1985, Bowyer et al. 1988).

To build the final model, I used true stepping with an alpha-to-enter = 0.050 and alpha-to-remove = 0.051 (Neter et al. 1985, Bowyer et al. 1988), and an all possible models approach, using both an adjusted multiple coefficient of determination (R_a^2) and Mallow's Cp statistic as selection criteria (Draper and Smith 1981: 294-380).

Vegetation

Between 4 and 7 June, 1988, I randomly located 9 plots, about 1.5 m^2 in size, adjacent to the Okpilak River and cleared them of snow. Peripheries of all plots were clearly marked. One Eriophorum vaginatum tussock per plot was sampled every 24 h. The length from basal node to apex of all inflorescences on each tussock was measured and the tussock marked to prevent resampling. Additional tussocks adjacent to the plots were exposed and sampled immediately to provide inflorescence lengths from tussocks with no exposure to the sun. These tussocks were also marked to prevent resampling.

RESULTS

Snowcover

Ten years of data from 1974 to 1987 were used in these analyses (Table 1); 1982, 1984, and 1985 were excluded because not all categories of snowcover were present on the coastal plain, and 1980 was excluded because no concentrated calving area was mapped. In only 3 years of 14 examined did >75% snow cover >50% of the available calving grounds (Table 1). Proportionally more area of >75% snowcover was used for concentrated calving, whereas proportionally less area of <25% snowcover was used for such activity (Table 2). A potential lack of precision in delimiting these areas, however, precludes direct statistical comparisons. Consequently, I compared the number of positive, zero, and negative

Table 1. Porcupine Caribou Herd available calving grounds snowcover. Parentheses enclose percent of area.

Year	>75% Snowcover km^2 (%)	25 -75% Snowcover km^2 (%)	<25% Snowcover km^2 (%)
1974	3,088 (20)	796 (5)	11,909 (75)
1975	10,752 (68)	1,934 (12)	3,106 (20)
1976	8,452 (54)	1,686 (11)	5,654 (36)
1977	7,484 (47)	4,664 (30)	3,645 (23)
1978	6,570 (42)	7,222 (46)	2,002 (13)
1979	1,524 (10)	1,564 (10)	12,706 (80)
1980[a]	8,559 (54)	4,128 (26)	3,106 (20)
1981	1,095 (7)	2,250 (14)	12,448 (79)
1982[a]	1,822 (12)	13,971 (88)	0 (0)
1983	1,353 (9)	7,802 (49)	6,638 (42)
1984[a]	0 (0)	4,419 (28)	11,374 (72)
1985[a]	0 (0)	0 (0)	15,793 (100)
1986	7,279 (46)	6,512 (41)	2,002 (13)
1987	6,794 (43)	5,480 (35)	3,518 (22)
Total[b]	64,772 (30)	62,428 (28)	93,901 (42)
Total[c]	54,391 (34)	39,910 (25)	63,628 (40)

[a] Year not used in analyses.

[b] Total includes all years from 1974 through 1987.

[c] Total excludes 1980, when no concentrated calving area was found, and 1982, 1984-1985, when not all snow categories were present.

Table 2. Porcupine Caribou Herd concentrated calving area snowcover by year. Parentheses enclose percent of area.

Year	>75% Snowcover km^2 (%)	25 -75% Snowcover km^2 (%)	<25% Snowcover km^2 (%)	Total area in km^2
1974	0 (0)	0 (0)	381 (100)	381
1975	1,839 (89)	78 (4)	147 (7)	2,064
1976	1,900 (84)	74 (3)	291 (13)	2,265
1977	1,340 (55)	356 (15)	724 (30)	2,420
1978	1,288 (83)	12 (1)	255 (16)	1,555
1979	413 (25)	330 (20)	912 (55)	1,655
1980	No concentrated calving area found			
1981	402 (20)	800 (39)	844 (41)	2,046
1982	0 (0)	914 (100)	0 (0)	914
1983	0 (0)	2,632 (79)	713 (21)	3,345
1984	0 (0)	762 (40)	1,138 (60)	1,900
1985	0 (0)	0 (0)	3,340 (100)	3,340
1986	550 (17)	920 (29)	1,700 (54)	3,170
1987	923 (46)	731 (37)	342 (17)	1,996
Total[a]	8,655 (32)	6,695 (25)	11,701 (43)	27,051
Total[b]	8,655 (41)	5,933 (28)	6,309 (30)	23,711

[a] Total includes all years from 1974 through 1987.

[b] Total excludes 1980, when no concentrated calving area was found, and 1982, 1984-1985.

indices of snowcover use for areas of >75% snowcover (category 1) with areas of <25% snowcover (category 3) within the concentrated calving area; significant differences occurred between levels of use and availability (G = 7.703, df = 2, P = 0.02). The preponderance of positive values for category 1 and majority of negative ones for category 3 (Table 3) indicated that inclusion of snow category 1 within the concentrated calving area was greater than its presence within the available calving area (i.e., female caribou selected areas with greater snowcover and neglected snow-free zones for concentrated calving activity).

Because of its relatively high use by parturient females, caribou use of snowcover category 1 was selected as the dependent variable for developing a regression model against weather data from Barter Island. Both true stepping and all-possible-regressions produced the same model with an R_a^2 = 0.817 (SE = 14.788, F = 21.112, P = 0.001).

$$\hat{Y} = 92.439 - 18.332X_1 + 0.255X_2$$

Where: $\hat{Y}$ = proportion of the concentrated calving area of >75% snowcover; X_1 = change in temperature (°C) on 3 June; and X_2 = depth (in mm) of snow on 30 May. I observed no evidence of skewness, kurtosis or lack of independence (multicollinearity) for variables included in the multiple regression, suggesting this model was apt.

Most temperature-based variables were correlated with change in temperature on 3 June (maximum r = 0.856) and summed temperature variables (thawing degree-days, etc.) were correlated with snow-variables. Snow-variables were strongly intercorrelated (maximum r = 0.991).

Standardized coefficients of regression for X_1 (-0.786) and X_2 (+0.631) indicated temperature factors contributed slightly more to the model than did snow depths. Relatively slight differences between the partial regression coefficients (-16.00 and +0.20) and the full coefficients in the model indicate that the two variables bring substantially different information to this model. Based on the large F-value, this relationship is highly predictive (Draper and Smith 1981),

Table 3. Snowcover use index. (Observed/Expected)-1. Observed use is the percent of the concentrated calving area in a given snow category. Expected use is the proportion of that snow category within the potential calving area.

Year	>75% Snowcover km^2 (%)	25 -75% Snowcover km^2 (%)	<25% Snowcover km^2 (%)
1974	-1.00	-1.00	0.33
1975	0.31	-0.67	-0.65
1976	0.56	-0.73	-0.64
1977	0.17	-0.50	0.30
1978	0.98	-0.98	0.23
1979	1.50	1.00	-0.31
1980	No concentrated calving area found		
1981	1.86	1.79	-0.48
1982	-1.00	0.14	a
1983	-1.00	0.61	-0.50
1984	a	0.43	-0.17
1985	a	a	1.00
1986	-0.63	-0.29	3.15
1987	0.07	0.06	-0.23

[a]Snow cover category not available.

and should be useful in determining the relative amount of area with >75% snowcover where concentrated calving occurs.

Areas of >75% snowcover usually appeared as a solid snowfield on satellite imagery. Small bare spots, often only tens of meters squared, and thus well below the 1 km^2 resolution of the satellite imagery, were widely scattered throughout the snowfields (Fig. 3). The presence of bare spots undetected by the satellite imagery likely resulted in slight overestimation of snowcover on the concentrated calving areas. From the first appearance of sufficient melt to be classed as 75 - 25%, the transition to >25% usually took 7-10 days.

Ground-based 35 mm photographs taken opportunistically from 30 May to 5 June in different years were compared with snow categories assigned from satellite imagery. These photographs showed that areas of >75% snowcover was not a uniform, unbroken field of snow. Model variables -- amount of daily temperature change and depth of snow measured at Barter Island -- probably index the number, size, and duration of bare spots in snowfields.

Vegetation

Eriophorum inflorescences elongated rapidly after release from snowcover (Table 4). After 18 to 24 h, most inflorescences protruded above the surrounding dead leaves of the tussock. Examination of tussocks about 8 h after removing the snowcover showed additional inflorescences not originally sampled, indicating that some inflorescences were hidden beneath the frozen surface of the tussock. Thus, it is probable that the mean length of day 0 inflorescences (Table 4) is shorter than indicated. No data were available on inflorescence growth after 2 days because rock ptarmigan (Lagopus mutus) ate all the unsampled Eriophorum inflorescences in all plots on the second day of sampling.

DISCUSSION

A strong positive association occurred between zones with greater snowcover and areas of concentrated calving by caribou on the arctic

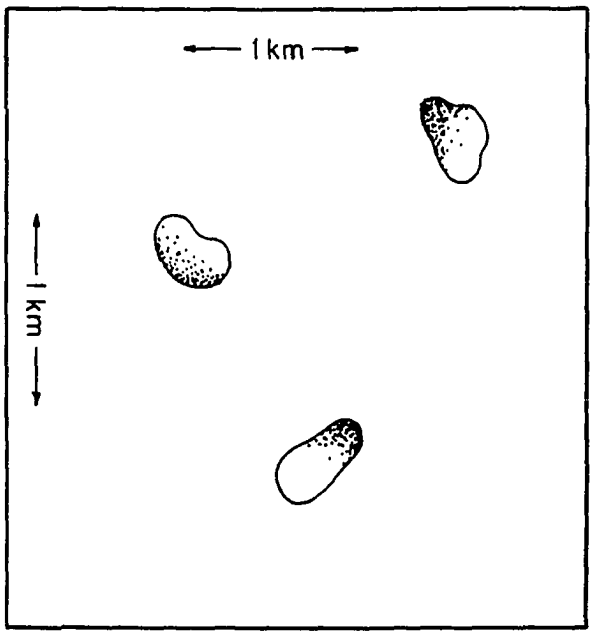

Figure 3. Small areas of bare ground are not detected by Tiros-N imagery within the 1 km^2 pixel resolution as simulated in this example.

Table 4. Eriophorum vaginatum inflorescence lengths after removal of snowcover.

	Time after removal of snowcover in days		
	0	1	2
N	22	47	11
$\bar{X}$ ± SD (mm)	60.2 ± 7.8	72.2 ± 11.1	85.6 ± 14.1
range (mm)	44 - 71	52 - 94	68 - 124
95% C.I. (mm)	59.0 - 61.4	71.2 - 73.2	83.4 - 87.8

coastal plain. This finding contradicts previous notions (Lent 1980) that large, snow-free zones are heavily used for calving, and supports other findings (Fleck and Gunn 1982). Use of areas of >75% snowcover for concentrated calving activity was directly related to the amount of snow on the ground and inversely related to temperature. Two potential causes may explain this positive relationship; nutrition and predation. These are not mutually exclusive, although the relative influence of one cause over the other may vary with time and the population dynamics of the PCH.

The first hypothesis is that snowmelt controls the availability and nutritional level of early greening plants and therefore the nutritional status of lactating females. Depth of the snow on the ground probably regulates both number and size of bare spots in snowfields. Usual minimum daily temperature during calving is below freezing; large fluctuations in daily temperature increase both absolute rise in temperature and the time-interval above freezing. Thus, large temperature fluctuations would increase the rate of snowmelt, whereas smaller ones would decrease this rate. Depth of snow prior to initiation of melting would control the duration of snowmelt and consequent availability of snow-free patches within snowfields.

Caribou apparently prefer to give birth on bare ground rather than on snow (Kelsall 1968, Skoog 1968, Lent 1980), and parturient females use these snow-free patches within snowfields on the concentrated calving area, often one cow per bare patch when openings are small (F. J. Mauer, USFWS, pers. commun.; pers. obs.). Observations from both the ground and the air indicated that calves were well concealed within these irregular patches. Thomson (1977) reported that wild reindeer also selected bare areas for calving, often at the edge of snow-covered ground.

Post-parturient caribou must optimize nutrient and energy allocation between lactation and maintaining their own body reserves. Females must meet nutritional requirements for lactation to insure growth of new-born calves (Rognmo et al. 1983, White and Luick 1984). Caribou are more

likely to conceive at mating when their body-weights are high, indicating good physical condition (Thomas 1982, Reimers 1983a, White 1983, Tyler 1987, R. D. Cameron, AK Dept. Fish and Game, unpubl. data). Thus, females must ingest sufficient forage to minimize weight losses while also meeting demands of lactation. Selection of areas with highly nutritious forage in a sufficient density to minimize search time and maximize food intake (Kelsall 1968; Klein 1970, 1982; Kuropat and Bryant 1980; White and Trudell 1980a, 1980b; Trudell and White 1981; Kuropat 1984) would be advantageous for lactating females. Inflorescences of Eriophorum vaginatum, a common tussock sedge on the coastal plain (Garner and Reynolds 1986), fulfill these forage requirements.

The regression model indicates that snowfields would be included in the concentrated calving area proportionally more often when rate of snowmelt was slower and, consequently, bare spots of smaller size. I hypothesize that the negative coefficient for temperature change and positive coefficient for snow depth in the regression model reflect the importance of an extended time of snowmelt to calving caribou; the slightly greater contribution of temperature to the model likewise reflects this importance.

At early snowmelt, Eriophorum inflorescences are at their maximum levels of N, P, lowest in percent acid detergent fiber, and low in phenols (Kuropat and Bryant 1980, Whitten and Cameron 1980, Kuropat 1984). Nutrient levels and digestibility are highest at the floral-bud stage and decline steadily thereafter. Dry matter digestibility, P, and N are at their lowest levels and acid detergent fiber is highest at anthesis (Whitten and Cameron 1980, Kuropat 1984), which occurs less than two weeks after snowmelt. As snow melts, it exposes more Eriophorum and reduces or eliminates energy expenditure of cratering by caribou for food and density of flower heads maximizes eating rate (Fancy and White 1985, Fancy 1986). Further, I postulate that dynamics of snowmelt provide Eriophorum inflorescences in early stages of growth for a longer period of time than

in areas totally free of snow. This condition would allow caribou to feed selectively on nutritious vegetation, and is analogous to Klein's (1982) observations concerning the influence of topographic variation and vegetation phenology on forage quality for caribou. Pegau (1968) and Wright (1979) noted that reindeer on the Seward Peninsula forage on inflorescences of Eriophorum vaginatum during green-up and track early phenological stages of vegetation as other plants become available. Eriophorum vaginatum is not common on the normal calving grounds of the Denali Herd, but the females use early greening plants intensively (Boertje 1981, 1984). Indeed, Fleck and Gunn (1982) postulated that similar patterns of snowmelt increased availability of nutritious forage for caribou in the Northwest Territories.

Competition for early season inflorescences of Eriophorum vaginatum also may influence choice of calving sites by caribou. The rapidity with which ptarmigan located my plots and consumed the inflorescences suggests the potential for competition for food between ptarmigan and caribou, as noted by Kuropat (1984). After 18 to 24 h, most Eriophorum inflorescences sampled had protruded above the surrounding dead leaves of the tussock and would have been available to selective grazers, such as caribou. On my study area, I noticed only 4 ptarmigan, but these few birds were able to strip all plots of inflorescences in less than 12 h. I saw ptarmigan flocks of >2000 birds farther west in the Brooks Range in 1987, and this number of birds likely could strip all available bare spots in a snowfield of Eriophorum in a short time. Proximity to freshly exposed Eriophorum would give caribou competitively advantageous access to inflorescences in years when ptarmigan populations are high, and particularly so in years when Eriophorum vaginatum production is low.

Caribou use of bare spots in a generally snow-covered area on the coastal plain also agrees with three ideas proposed by Bergerud and Page (1987) for successfully avoiding predators. Caribou using bare spots on the coastal plain are: 1) not on normal travel-routes of predators and are

displaced from alternate prey, such as ground squirrels (Spermophilus parryii) and arvicolid rodents (Babcock 1986, Garner and Reynolds 1986); 2) relatively dispersed, increasing searching time by predators and reducing opportunities for surplus killing (Miller et al. 1985), especially when bare spots are small; and 3) against a mottled background, with crypsis further enhanced by the contrast between bare ground and snow. Snowfields also might discourage avian predation because of damping effects on thermals used for soaring by birds of prey, thereby shifting the normal travel routes of avian predators away from calving caribou. Although calves are highly precocious (Murie 1932, Lent 1974), considerable losses to predation can occur on the calving grounds (Miller and Broughton 1974; Miller et al. 1985; Fancy and Whitten, in press).

Both predator avoidance and nutritional factors would, in the long term, lead to selection of bare spots in snowfields as calving sites by female caribou. Thus, it is not possible from my results to determine whether nutrition or predator avoidance factors exert the greater selective pressure, if, indeed, either pressure exceeds the other.

AUTUMN MIGRATION

INTRODUCTION

Following calving on the arctic coastal plain of northeastern Alaska and northwestern Canada in late May and June, females of the PCH rear their calves on the plain or in adjacent foothills of the Brooks Range during June and early July (Jakimchuk et al. 1974, Roseneau et al. 1975, Surrendi and DeBock 1976). Dispersal usually occurs in late July and August, with some PCH animals remaining on the coastal plain and others moving south of the Brooks Range into both Alaska and the northern Yukon Territory, Canada (Roseneau et al. 1975, Surrendi and DeBock 1976, Thompson 1978, Ealey 1980). Autumn migration generally is considered to begin in September and end between late October and December (Jakimchuk et al. 1974, Roseneau et al. 1975, Surrendi and DeBock 1976, Thompson 1978, Ealey 1980, Whitten and Cameron 1983).

Prior to detailed studies using radio- and satellite-collared caribou, the PCH was thought to follow four basic routes in its autumn migration (Urquhart 1983). The first was from the British and Barn Mountains in northern Yukon Territory south across the Porcupine River to the Ogilvie and surrounding mountain ranges (Thompson 1978, Ealey 1980). The second was south along the Richardson Mountains which straddle the northeastern border of Yukon and Northwest Territories, and across the Peel River to the Hart, Wind, and Blackstone rivers, and adjacent drainages (Thompson 1978). The third route followed the Alaska - Canada border south, then separated east and west to drainages in Canada and Alaska (Surrendi and DeBock 1976). The final route was south through the Brooks Range in Alaska to the drainage of the Chandalar River (McCourt et al. 1974, Roseneau and Stern 1974, Whitten and Cameron 1983). These routes (Fig. 4) were not a single series of trails, but rather a complex set of corridors, not all of which were used equally by migrating caribou

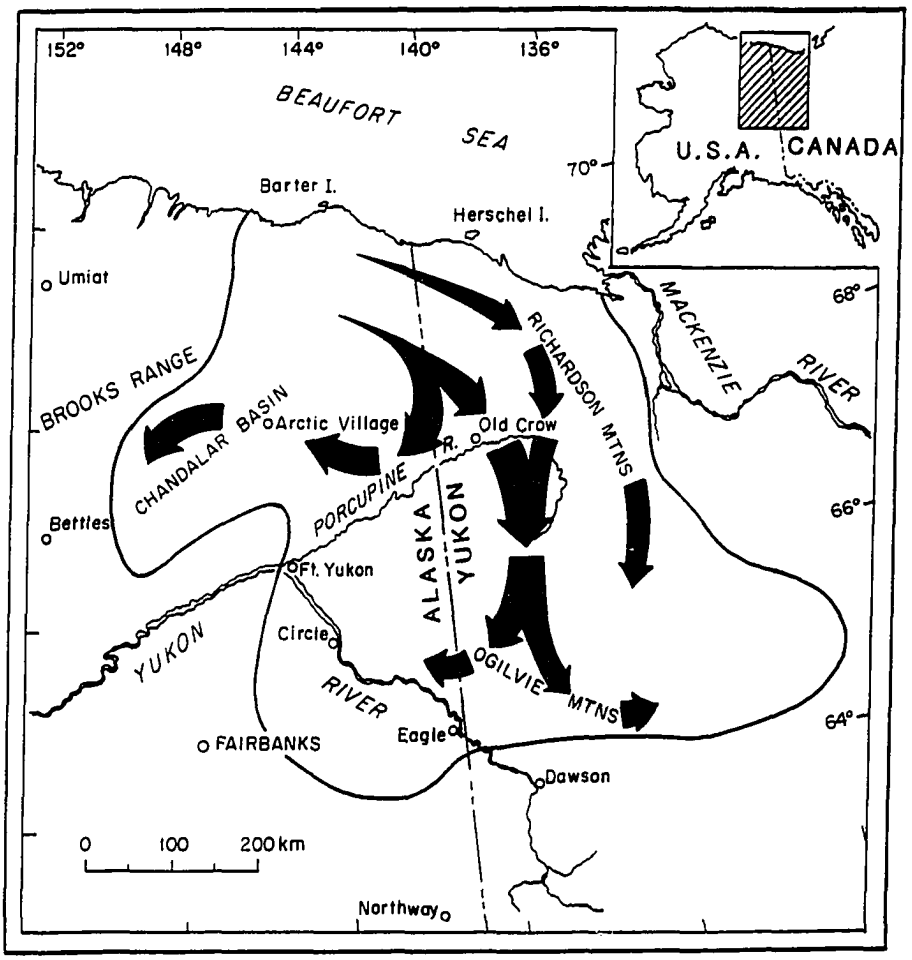

Figure 4. Autumn migration routes of the PCH (adapted from Urquhart 1983).

(Urquhart 1983).

Anecdotal accounts attribute impetus for autumn migrations of the PCH to snowstorms and sudden decreases in temperature (Banfield 1954a, 1954b; Kelsall 1968; Jakimchuk et al. 1974; McCourt et al. 1974; Surrendi and DeBock 1976; Thompson 1978). Migration may stall and be temporarily reversed when initial snowfall ceases, then resume with continued storms (Jakimchuk et al. 1974, Surrendi and DeBock 1976, Curatolo and Roseneau 1977, Thompson 1978, Ealey 1980); therefore, decreasing temperatures and their rate of decrease appear to influence continuity of such movements. A large or rapid decrease in temperature early in September apparently results in lengthy autumn migrations (Kelsall 1968, Roseneau et al. 1975, Surrendi and DeBock 1976, Thompson 1978).

A seasonal predisposition to migration, perhaps related to photoperiod (Pendergast 1973), would explain why the occasional snow squall in summer does not initiate southward migration prematurely. The PCH migrates in the absence of September snowstorms, further suggesting a seasonal predisposition for migration. For example, in 1976 weather remained warm and the ground free of snow over the summer range of the PCH well into September (Curatolo and Roseneau 1977). Caribou remained widely dispersed, but slowly moved southward without coordinated movements (Curatolo and Roseneau 1977) that characterize autumn migrations.

Evidence for a directed and synchronous autumn movement in September is not extensive. Also, evidence that particular factors initiate migration are poorly documented; weather-imputed causes of migration are incidental observations, and quantification of caribou movements in relation to weather are scant. No consistent tracking of individual animals was done. Observers recorded weather conditions at the site and time caribou came into view and assumed that these conditions caused caribou movements, although caribou already may have been moving in

response to other, earlier, stimuli (Curatolo 1975). Nevertheless, that weather is the primary cause of autumn migration has become established without a critical test of this idea.

I tested the hypothesis that weather is a primary influence on the initiation and continuation of the autumn migration of the PCH using weather data from 1985, 1986, and 1987 and movement data from satellite collared caribou (Fancy et al. 1988, 1989). I evaluated the predictability of movements based upon weather during September and October.

METHODS

Data Collection

Weather data for September and October, 1985 - 1987 were obtained from 11 permanent weather stations within and near the range of the PCH. In Alaska, I obtained weather records for Barter Island, Bettles, Chandalar Lake, Circle City, Fort Yukon, Kuparuk, and Umiat (Natl. Oceanic and Atmos. Adm., Natl. Climatic Data Cent., Asheville, NC). Stations in Canada were located at Beaver Creek, Dawson City, Komakuk Beach, and Old Crow (Can. Climate Cent., Atmos. Environ. Serv., Downsview, Ontario, Can.; Table 5). Data recorded included Julian date, length of day (h), amount of daylight change from the previous day (h), maximum and minimum daily temperature (°C), amount of precipitation in water equivalent (mm), amount of snowfall (mm), and amount of snow on the ground (mm). Mean daily temperature (°C) and amount of daily change in temperature (°C) were derived from reported data and used as indices to cloudiness because data on cloud cover were not reported in monthly weather summaries. Wind was not used in these analyses. No uniform index to wind was derived because of the differences in wind vectors at various altitudes and effects of topography on ground-level winds. Additionally, wind is thought to have little effect on direction of travel by caribou (Banfield 1954b, Skoog 1968), except for times of intense insect harassment (Curatolo 1975, White et al. 1975).

Table 5. Location of weather stations that provided data for autumn migration analyses. Letters in parentheses are abbreviations used in text.

Station Name	North West Latitude	Longitude	Elevation (m)
Barter Island (BTI)[1]	70° 08′	143° 38′	13
Beaver Creek (BVR)[2]	62° 25′	140° 52′	649
Bettles (BTL)[1]	66° 55′	151° 31′	208
Chandalar Lake (CLK)[1]	67° 30′	148° 30′	595
Circle City (CCT)[1]	65° 50′	144° 04′	194
Dawson City (DAW)[2]	64° 03′	139° 08′	369
Eagle (EGL)[1]	64° 47′	141° 12′	275
Fort Yukon (FYK)[1]	66° 33′	145° 12′	143
Komakuk Beach (KKK)[2]	69° 35′	140° 11′	7
Kuparuk (KPK)[1]	70° 19′	149° 35′	21
Ogilvie River (OGV)[2]	65° 22′	138° 18′	579
Old Crow (OLC)[2]	67° 35′	139° 50′	253
Umiat (UMT)[1]	69° 22′	152° 08′	86

[1]Alaska [2]Canada

Photoperiod was determined (Carroll n.d.) for the center of the range of the PCH, at 67° N, 141° W. Widely scattered, changing locations of caribou with satellite collars precluded use of photoperiod variables derived from actual locations of animals. Use of the center of the PCH range provided an index to light regimes occurring throughout the distribution of the PCH with conditions changing slightly faster in the north and slower in the south.

Daily locations of female caribou were obtained using the Argos Data Collection and Location System (Fancy et al. 1988) for September and October of 1985, 1986, and 1987. Most collared caribou had ceased migratory movements by November; therefore no modeling was attempted beyond October.

Data Analysis

I tested the influence of weather on autumn migration of the PCH by multiple regression: rate and direction of movement (dependent variables) were modeled separately. Caribou movements are bipartite; they consist of amount of movement and direction of movement. Direction of movement was converted to sines to reflect west (sine = -1) and east (sine = 1) movements.

Data for the 3 years were pooled by month for modeling. Modeling by individual years was impractical because of reduced sample sizes and resulting limits on the variability of both movements and weather, and overparamaterization of some models.

Rate of movement ($km \cdot h^{-1}$) was calculated as the distance between successive locations divided by the time between locations. Actual distances moved by individual animals likely exceeded distances estimated by daily radio-locations (Bowyer 1981, Laundré et al. 1987), thus the estimated rates of movement were a minimum estimate. To pool data for individual caribou, the average rate of movement was calculated by month for each year, and the dependent variable in the models was based upon

deviations from this mean.

Assuming that daily movements exceeding the mean were most indicative of caribou migration, I modeled the proportion of animals moving >1 SD of the mean rate of movement. Number of animals for which daily rate of movement differed by >1 SD of the mean was divided by the total number of animals for that day and the resulting proportion became the dependent variable for the multiple linear regression models.

Models were built using data for those days for which rates of movement exceeded 1, 1.5, and 2 SD from the mean. Although 3 models were built, the dependent variables reflected the same pattern: caribou movements that differed from average.

Direction of movement was modeled by converting azimuths of movements to sines and cosines, then averaging these values for each day. Dispersed movements, with some caribou traveling east and others west, averaged near 0. Coordinated movements provided averages closer to east (1) or west (-1). Similar modeling using cosines for north (1) and south (-1) movements also was attempted, but no significant models were built using cosines.

Variables considered for the models were examined for multicollinearity and normality (Snedecor and Cochran 1980:78-81); those departing from assumptions for regression analysis were transformed (Snedecor and Cochran 1980:288-292). A Pearson correlation matrix was used as an informal test for independence of weather variables ($\underline{X}_i$). Variables with an absolute value of $\underline{r} \geq 0.7$ (appendix B) were not allowed to enter regression models concurrently. Additional formal testing for multicollinearity, including examination of tolerance (variance inflation factors) and partial coefficients of regression, was completed after the model was built (Neter et al. 1985, Bowyer et al. 1988).

To build final models, I used true stepping with an alpha-to-enter = 0.050 and alpha-to-remove = 0.051 (Neter et al. 1985, Bowyer et al. 1988), and an all-possible-models approach. Statistical procedures were

identical to those described in Eastland et al. (1989).

RESULTS

Plots of movements of caribou with satellite collars (Figs. 5 - 10) indicated that migration routes used varied among animals, within months, and among years. Routes followed by caribou corresponded only loosely with corridors described by Urquhart (1983). Direction of movements differed more among the beginning, middle, and end of September than during October (Figs. 5 - 10).

September

For September, apt models were built for movements >1 SD (Table 6; model 1), and >1.5 SD of the monthly mean (Table 6; model 2). A third model (Table 6; model 3) for movements >2 SD of the mean is presented primarily for explanatory purposes because the number of parameters is >10% of the sample size (Neter et al. 1985, Bowyer et al. 1988).

A trend ($R_a^2 \leq 0.403$, $P \leq 0.014$; Table 6) exists in September for collared caribou to move more than average when large differences between daily high and low temperatures occurred at Old Crow and Umiat (OLCCHGT, UMTCHGT), and lower temperatures at Bettles and Dawson (BTLMINT, DAWMINT). Standardized coefficients of regression of models for rate of movement (Table 6; models 1, 2, and 3) indicated that temperatures were the most important weather variables. Although differences were not great, mean daily temperatures at Dawson and Bettles (DAWAVGT, BTLAVGT) were lower and temperature flux at more northerly stations was lower for days on which rates of movement were higher (Table 7). Large changes in the amount of daylight (DAYCHG) also was related to increased movement rate. Amount of daylight change increases slightly as September progresses (6.45 min to 6.67 min at 67° N, 141° W). This change is negative (Table 7) because of the decrease in daylength; the regression coefficient has a positive coefficient (Table 6; model 2), indicating that increased movements occur early in the month. Because photoperiod (DAYCHG) entered 1 model for rate of movement (Table 6; model 2), I forced photoperiod into the model for

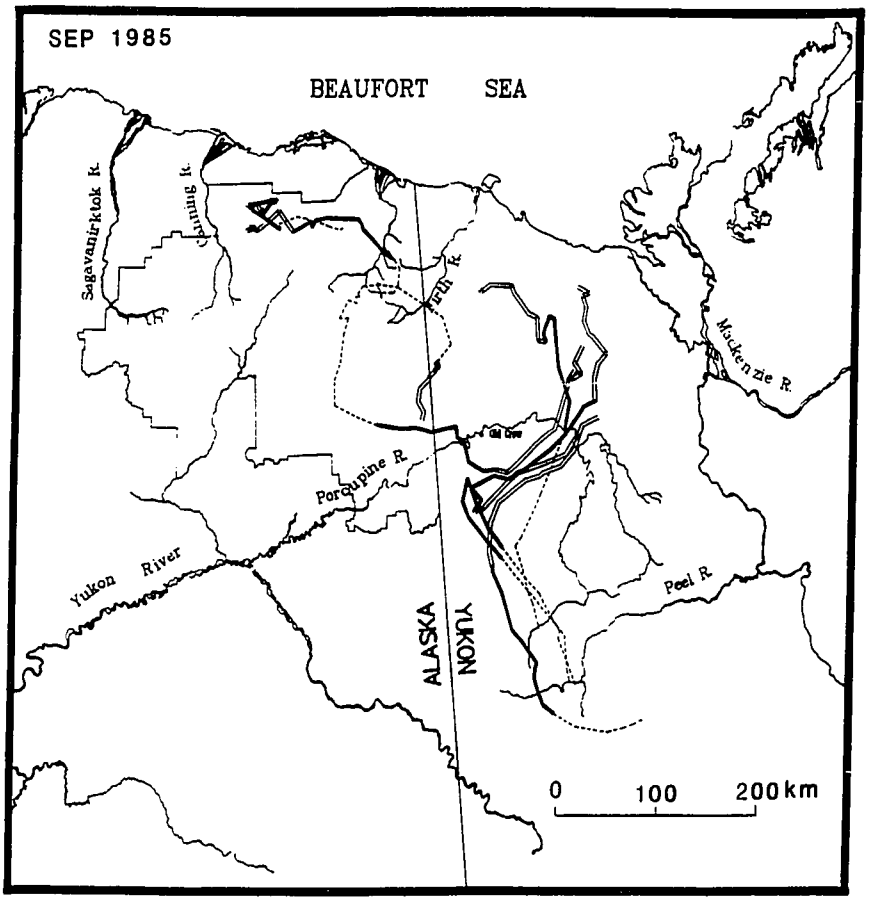

Figure 5. Movements of satellite collared caribou in September, 1985.

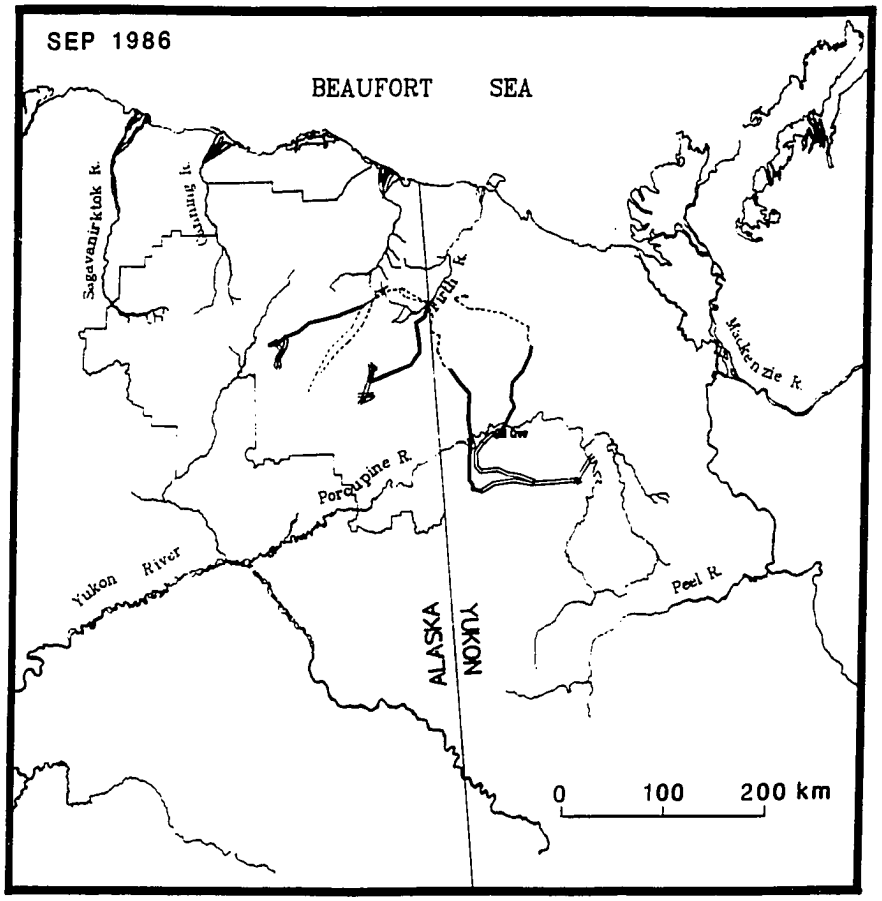

Figure 6. Movements of satellite collared caribou in September, 1986.

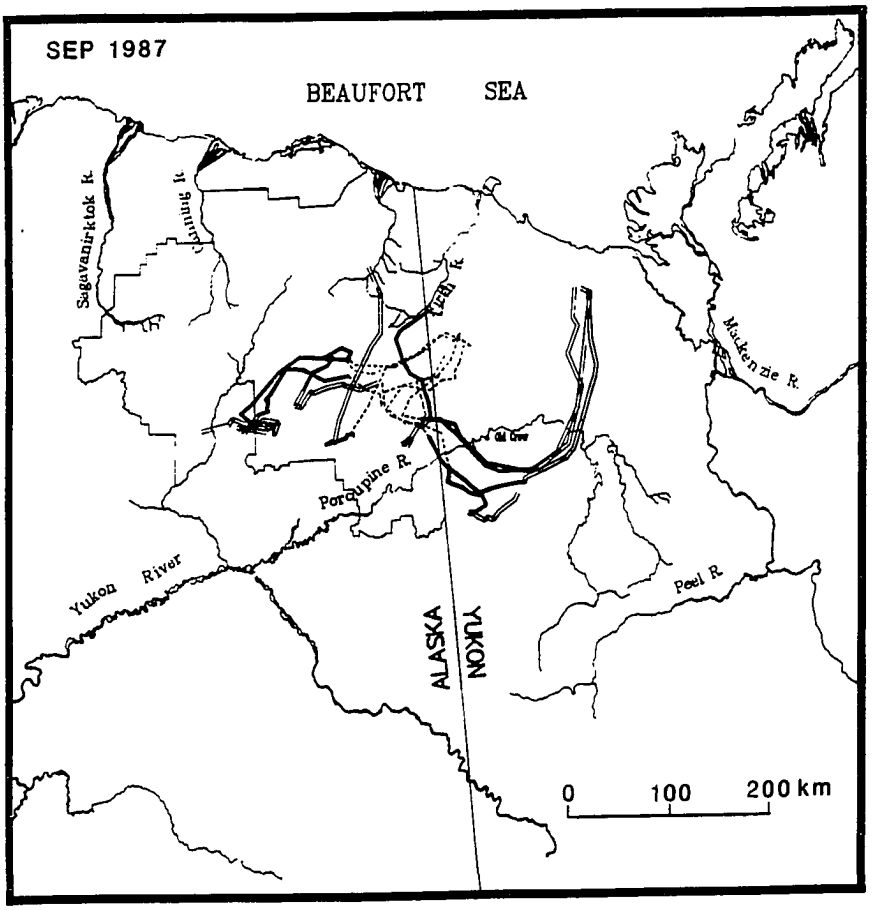

Figure 7. Movements of satellite collared caribou in September, 1987.

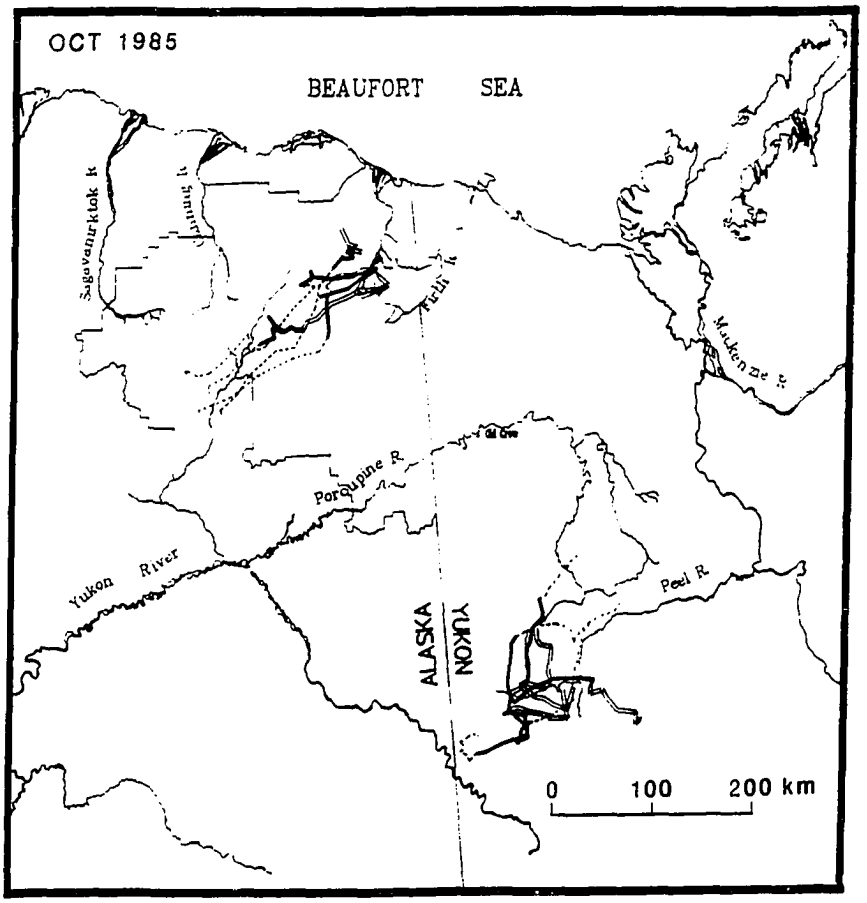

Figure 8. Movements of satellite collared caribou in October, 1985.

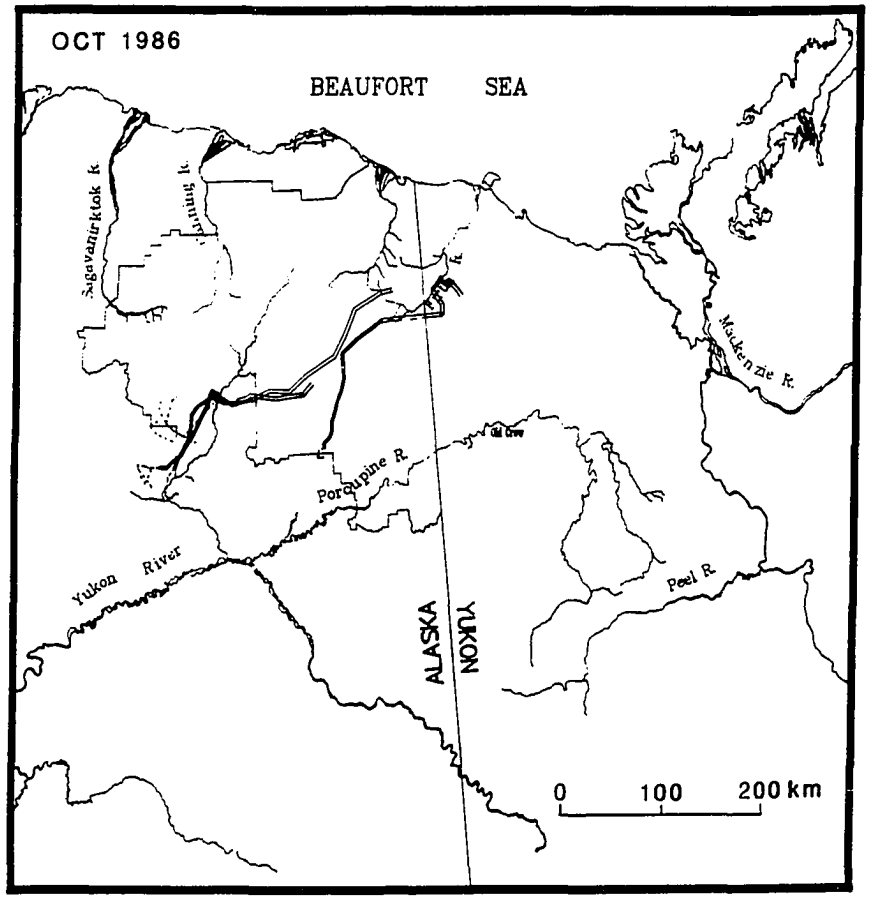

Figure 9. Movements of satellite collared caribou in October, 1986.

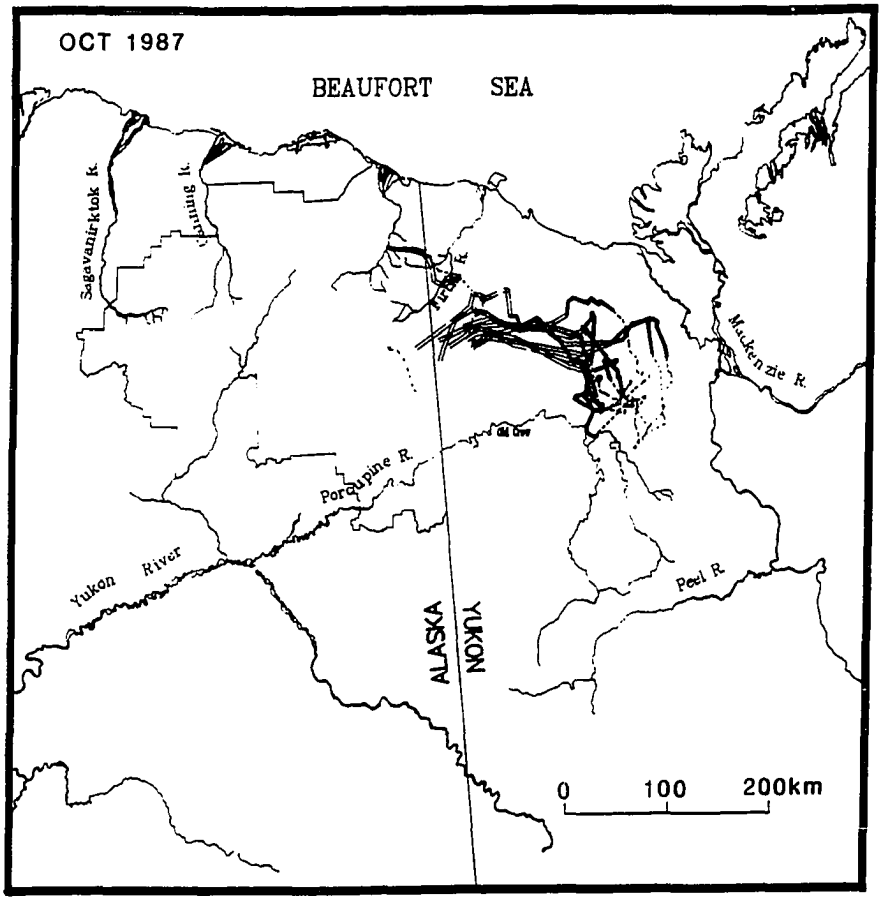

Figure 10. Movements of satellite collared caribou in October, 1987.

Table 6. Models for rate of movement in September, 1985 -1987.

Model 1. $\hat{Y} = 0.3167 + 0.0060X_1 + 0.0153X_2 - 0.0253X_3$

($R_a^2 = 0.206$; SE = 0.111; df = 3, 44; F = 5.058; P = 0.004)

Where:

$\hat{Y}$ = Proportion of the collared animals moving >1 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion >0 were used.

X_1 = Difference (°C) between daily minimum and maximum temperatures at Old Crow, Yukon Territory (OLCCHGT).

X_2 = Minimum daily temperature (°C) at Barter Island, Alaska (BTIMINT).

X_3 = Average daily temperature (°C) at Bettles, Alaska for the day on which movement occurred (BTLAVGT).

Variable	Standardized Coefficients
X_1 (OLCCHGT)	0.202
X_2 (BTIMINT)	0.366
X_3 (BTLAVGT)	-0.692

Table 6 (continued). Models for rate of movement in September, 1985 - 1987.

Model 2. $\hat{Y} = 4.8447 + 0.6916X_1 - 0.0177X_2 + 0.0066X_3$

($R_a^2 = 0.366$; SE = 0.077; df = 3, 27; F = 6.774; P = 0.001)

Where:

$\hat{Y}$ = Proportion of the collared animals moving >1.5 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion >0 were used.

X_1 = Difference in number of daylight minutes from the previous day (DAYCHG).

X_2 = Average temperature (°C) at Dawson City, Yukon Territory for the day on which movement occurred (DAWAVGT).

X_3 = Difference (°C) between daily minimum and maximum temperatures at Umiat, Alaska (UMTCHGT).

Variable	Standardized Coefficients
X_1 (DAYCHG)	0.492
X_2 (DAWAVGT)	-0.692
X_3 (UMTCHGT)	0.293

Table 6 (continued). Models for rate of movement in September, 1985 - 1987.

Model 3. $\hat{Y} = 0.1348 + 0.0056X_1 - 0.0067X_2$

($R_a^2 = 0.403$; SE = 0.050; df = 2, 13; F = 6.062; P = 0.014)

Where:

$\hat{Y}$ = Proportion of the collared animals moving >2 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion > 0 were used.

X_1 = Maximum daily temperature (°C) at Umiat, Alaska (UMTMAXT).

X_2 = Minimum daily temperature (°C) at Dawson City, Yukon Territory (DAWMINT).

Variable	Standardized Coefficients
X_1 (UMTMAXT)	0.484
X_2 (DAWMINT)	-0.464

Table 7. Values of variables in the models for September, 1985 - 1987.

Variable[1]	All days $\bar{X} \pm SD$ n = 90	Days on which at least 1 animal moved more than the specified SD above the average rate in km/h: 1 $\bar{X} \pm SD$ n = 48	1.5 $\bar{X} \pm SD$ n = 31	2 $\bar{X} \pm SD$ n = 16
DAYLONG	13.1 ± 1.1	13.3 ± 1.0	13.2 ± 1.0	13.5 ± 0.9
DAYCHG	-6.6 ± 0.1	-6.6 ± 0.1	-6.6 ± 0.1	-6.6 ± 0.1
BTIMINT	-1.6 ± 3.2	-1.9 ± 3.0	-1.7 ± 2.6	-0.9 ± 2.2
BTLAVGT	4.0 ± 3.6	3.3 ± 3.4	3.2 ± 3.5	3.5 ± 3.9
BVRCHGT	12.7 ± 6.1	11.9 ± 5.8	11.7 ± 5.8	13.2 ± 6.8
DAWAVGT	5.5 ± 3.5	5.1 ± 3.5	5.4 ± 3.8	5.9 ± 3.7
DAWMINT	-1.0 ± 4.1	-1.3 ± 4.2	-1.0 ± 4.3	-1.3 ± 4.5
KKKCHGT	7.3 ± 4.2	6.8 ± 3.4	6.1 ± 3.5	6.5 ± 4.0
OLCCHGT	9.5 ± 4.8	8.9 ± 4.2	8.8 ± 4.9	10.1 ± 5.6
UMTCHGT	8.4 ± 4.2	8.0 ± 4.0	7.7 ± 4.3	7.6 ± 4.2
UMTMAXT	5.2 ± 5.8	4.3 ± 4.7	3.9 ± 4.8	5.2 ± 5.6

[1]DAYLONG = Day length in hours.

DAYCHG = Change in length of day from previous day in minutes.

BTI = Barter Island
BTL = Bettles
BVR = Beaver Creek
DAW = Dawson City
FYK = Fort Yukon
KKK = Komakuk Beach
OLC = Old Crow
UMT = Umiat

MINT = Minimum daily temperature (°C).

MAXT = Maximum daily temperature (°C).

AVGT = Average daily temperature (°C).

CHGT = absolute difference between MINT and MAXT (°C).

rate of movement >1 SD to evaluate its contribution. The standardized coefficient of regression was -0.027, <10% of any of the weather variables, suggesting that photoperiod is relatively unimportant in influencing rate of movement in September.

For directional movement in September, collared caribou tended to move east when daylength (DAYLONG) was shorter, or when large differences occurred between daily temperature highs and lows at Beaver Creek (BVRCHGT), and small temperature differences occurred at Komakuk Beach (KKKCHGT) (Table 8; model 1). Standardized coefficients of regression (Table 8) suggest that BVRCHGT is the most important weather factor in influencing directional movements in September, with temperature flux at Komakuk Beach and photoperiod equal, but of lesser overall importance. These weather factors are probably different from those that increase daily movements, because the model was less significant on days when some proportion of the herd moved more than average (Table 8; model 2, model 3).

October

In October, a trend for decreased rate of movement (Table 9; model 1) occurred early in the month when daylengths (DAYLONG) were longer and amount of snow on ground at Chandalar Lake, Alaska (CLKSOG) was relatively great (Table 10). Amount of snow on ground was of greater importance than timing, as reflected by the standardized coefficients of regression (Table 9; model 1). Differences among 1985 - 1987 mean amount of snow on ground at Chandalar Lake for days on which a portion of the collared caribou moved <1 SD and days on which a portion moved >1 SD are not great, but the difference may be biologically significant (Parker et al. 1984, Klein et al. 1987), especially for smaller animals (i.e. calves). Increased movement occurred (Table 9; model 2, model 3) later in October (DAYLONG) when daily temperature fluctuations were greater at Barter Island (BTICHGT) and Bettles (BTLCHGT) in Alaska and at Komakuk Beach (KKKCHGT) in Canada. Photoperiod had the strongest influence for

Table 8. Models for east-west deviation in movement during September, 1985 - 1987. Direction: positive $\hat{Y}$ = easterly; negative $\hat{Y}$ = westerly.

Model 1. $\hat{Y} = 1.0285 - 0.0883X_1 + 0.0235X_2 - 0.0221X_3$

($R_a^2 = 0.161$; SE = 0.335; df = 3, 86; F = 6.690; P < 0.001)

Where:

$\hat{Y}$ = Deviation of movement of collared animals from a north-south line.

X_1 = Length of day at 67° N, 141° W (DAYLONG).

X_2 = Difference (°C) between minimum and maximum temperatures at Beaver Creek, Yukon Territory (BVRCHGT).

X_3 = Difference (°C) between minimum and maximum temperatures at Komakuk Beach, Yukon Territory (KKKCHGT).

Variable	Standardized Coefficients
X_1 (DAYLONG)	-0.258
X_2 (BVRCHGT)	0.390
X_3 (KKKCHGT)	-0.253

Table 8 (continued). Models for east-west deviation in movement during September. Direction: positive $\hat{Y}$ = easterly; negative $\hat{Y}$ = westerly.

Model 2. $\hat{Y} = 0.9856 - 0.0778X_1 + 0.0143X_2 - 0.0239X_3$

($R_a^2 = 0.069$; SE = 0.312; df = 3, 44; F = 2.169; P = 0.105)

Where:

$\hat{Y}$ = Deviation of movement of collared animals from a north-south line. Only those days on which a proportion of the collared animals moved > 1 SD of the $\bar{X}$ rate of travel (km·h) were used.

X_1, X_2, X_3 = Same as in original model.

Model 3. $\hat{Y} = 1.1702 - 0.0868X_1 + 0.0041X_2 - 0.0206X_3$

($R_a^2 = 0.000$; SE = 0.312; df = 3, 27; F = 0.995; P = 0.410)

Where:

$\hat{Y}$ = Deviation of movement of collared animals from a north-south line. Only those days on which a proportion of the collared animals moved > 1.5 SD of the $\bar{X}$ rate of travel (km·h) were used.

X_1, X_2, X_3 = Same as in original model.

Table 9. Models for rate of movement in October, 1985 -1987.

Model 1. $\hat{Y} = -3.4963 + 0.4150X_1 + 0.0035X_2$

($R_a^2 = 0.368$; SE = 0.672; df = 2, 76; F = 23.703; P < 0.001)

Where:

$\hat{Y}$ = Proportion of the collared animals moving <1 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion > 0 were used.

X_1 = Length of day at 67° N ,141° W (DAYLONG).

X_2 = Snow on ground (mm) at Chandalar Lake, Alaska (CLKSOG).

Variable	Standardized Coefficients
X_1 (DAYLONG)	0.578
X_2 (CLKSOG)	0.651

Table 9 (continued). Models for rate of movement in October, 1985 -1987.

Model 2. $\hat{Y} = -0.3427 + 0.0665X_1 - 0.0100X_2 + 0.0285X_3 + 0.0184X_4$

($R_a^2 = 0.280$; SE = 0.158; df = 4, 48; F = 6.04; P < 0.001)

Where:

$\hat{Y}$ = Proportion of the collared animals moving >1 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion >0 were used.

X_1 = Length of day at 67° N, 141° W (DAYLONG).

X_2 = Difference (°C) between minimum and maximum daily temperatures at Beaver Creek, Yukon Territory for the day on which movement occurred (BVRCHGT).

X_3 = Amount of daily precipitation (mm) at Circle City, Alaska. Snow was melted prior to measurement (CCTPPT).

X_4 = Difference (°C) between daily minimum and maximum temperatures at Barter Island, Alaska (BTICHGT).

Variable	Standardized Coefficients
X_1 (DAYLONG)	0.415
X_2 (BVRCHGT)	-0.283
X_3 (CCTPPT)	0.180
X_4 (BTICHGT)	0.330

Table 9 (continued). Models for rate of movement in October, 1985 -1987.

Model 3. $\hat{Y} = 0.0534 + 0.0180X_1 + 0.0104X_2$

($R_a^2 = 0.299$; SE = 0.079; df = 2, 19; F = 5.470; P = 0.013)

Where:

$\hat{Y}$ = Proportion of the collared animals moving >2 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion >0 were used.

X_1 = Difference (°C) between minimum and maximum daily temperatures at Bettles, Alaska (BTLCHGT).

X_2 = Difference (°C) between minimum and maximum daily temperatures at Komakuk Beach, Yukon Territory (KKKCHGT).

Variable	Standardized Coefficients
X_1 (BTLCHGT)	0.387
X_2 (KKKCHGT)	0.471

Table 10. Values of variables in models for October, 1985 - 1987.

Variable[1]	All days $\bar{X} \pm SD$ n = 93	Days on which at least 1 animal moved more than the specified SD from the average rate in km/h: -1 $\bar{X} \pm SD$ n = 87	+1 $\bar{X} \pm SD$ n = 54	+2 $\bar{X} \pm SD$ n = 22
DAYLONG	9.4 ± 1.1	9.3 ± 1.1	9.4 ± 1.2	9.7 ± 1.3
DAYCHG	-6.5 ± 0.1	-6.5 ± 0.1	-6.5 ± 0.1	-6.5 ± 0.1
BTICHGT	6.1 ± 3.9	6.2 ± 4.0	5.7 ± 3.6	6.6 ± 4.1
BTISF	10.7 ± 28.5	11.3 ± 29.4	11.1 ± 30.2	11.8 ± 38.5
BTISOG	61.1 ± 72.1	64.1 ± 73.5	49.3 ± 70.2	56.8 ± 77.0
BTLCHGT	6.7 ± 3.0	6.9 ± 3.0	6.6 ± 2.6	6.8 ± 2.0
BVRCHGT	10.8 ± 4.9	10.8 ± 4.9	10.7 ± 5.2	10.7 ± 5.5
CCTPPT	0.8 ± 3.0 (n = 90)	0.8 ± 3.1 (n = 84)	0.3 ± 1.2 (n = 53)	0.6 ± 1.8
CLKSOG	165.4 ± 154.0 (n = 85)	171.2 ± 157.6 (n = 79)	122.9 ± 129.1 (n = 48)	114.0± 141.1 (n = 21)
KKKCHGT	7.0 ± 3.6	7.1 ± 3.6	6.8 ± 3.4	7.6 ± 4.3

[1]DAYLONG = Day length in hours.

DAYCHG = Change in length of day from previous day in minutes.

BTI = Barter Island BTL = Bettles BVR = Beaver Creek
CCT = Circle City CLK = Chandalar Lake KKK= Komakuk Beach

AVGT = Average daily temperature (°C).

CHGT = Absolute difference between minimum and maximum daily temperature (°C).

PPT = Precipitation (mm): snow is melted prior to measurement.

SOG = Snow on ground (mm).

SF = Snowfall (mm).

movement rates >1 SD of the mean (Table 9; model 2), yet it failed to enter the model for >2 SD (Table 9; model 3). Consequently, I forced DAYLONG into the model for >2 SD above the mean rate of movement. Forcing the photoperiod variable overparameterized the model (Neter et al. 1985, Bowyer 1988), so the absolute values of the standardized coefficient of regression may not be reliable. Nonetheless, standardized coefficients for BTLCHGT and KPKCHGT (0.476 and 0.439, respectively) both ranked higher than for DAYLONG (0.392). Intercorrelation (lack of independence among variables) prevented modeling movements of 1.5 SD above the average October rate of travel (0.335 ± 0.267 km·h^{-1}).

Satellite-collared caribou moved east (Table 11; model 1) early in the month when amount of daylight change (DAYCHG) was larger and daily temperature fluctuations were greater at Beaver Creek (BVRCHGT). Westward movements occurred when it was snowy at Barter Island, Alaska (BTISOG, BTISF), and temperatures fluctuated during the day at Komakuk Beach, Yukon Territory (KKKCHGT). Similarity of weather conditions during increased rate of movement to those correlating with directional movement is indicated by significance of the directional model when applied only to days in which movement was >1 SD from the mean rate of travel (Table 11; models 2, 3). These weather factors are similar to those correlated with directional movements in September.

Type I errors whereby the null hypothesis is falsely rejected in about 5% of statistical tests of data (Snedecor and Cochran 1980) suggest that some multiple linear regression models may have been significant although the correlations contained within them were caused by chance (Wilkinson 1988). To explore this likelihood, I used a random number generator and generated 60 sets of data for variables in the October model for proportion of the collared animals moving >1 SD of the monthly mean (Table 9; model 2). Of 60 models generated with random values in the range for each variable found in the actual model, 2 were significant ($P < 0.05$). The 2 significant models were the only ones of the 60 to have

Table 11. Models for east-west deviation in movement during October, 1985 - 1987. Direction: positive $\hat{Y}$ = easterly; negative $\hat{Y}$ = westerly.

Model 1. $\hat{Y} = 8.7321 + 1.3300X_1 + 0.0182X_2 - 0.0267X_3 - 0.0025X_4 - 0.0022X_5$

($R_a^2 = 0.330$; SE = 0.370; df = 5, 87; F = 10.054; P < 0.001)

Where:

$\hat{Y}$ = Deviation of movement of collared animals from a north-south line.

X_1 = Change in length of day from previous day at 67° N, 141° W (DAYCHG).

X_2 = Difference (°C) between minimum and maximum temperatures at Beaver Creek, Yukon Territory (BVRCHGT).

X_3 = Difference (°C) between minimum and maximum temperatures at Komakuk Beach, Yukon Territory (KKKCHGT).

X_4 = Amount of snow on ground (mm) at Barter Island, Alaska (BTISOG).

X_5 = Amount of daily snowfall (mm) at Barter Island, Alaska (BTISF).

Table 11 (continued). Models for east-west deviation in movement during October, 1985 - 1987. Direction: positive $\hat{Y}$ = easterly; negative $\hat{Y}$ = westerly.

Model 1. continued.

Variable	Standardized Coefficients
X_1 (DAYCHG)	0.372
X_2 (BVRCHGT)	0.195
X_3 (KKKCHGT)	-0.212
X_4 (BTISOG)	-0.394
X_5 (BTISF)	-0.138

Model 2. $\hat{Y} = 8.2273 + 1.2450X_1 + 0.0159X_2 - 0.0249X_3 - 0.0026X_4 - 0.0024X_5$

($R_a^2 = 0.332$; SE = 0.368; df = 5, 81; F = 9.559; P < 0.001)

Where:

$\hat{Y}$ = Deviation of movement of collared animals from a north-south line. Only those days on which a proportion of the collared animals moved <1 SD of the $\bar{X}$ rate of travel (km·h-1) were used.

X_1, X_2, X_3, X_4, X_5 = Same as in original model.

Table 11 (continued). Models for east-west deviation in movement during October, 1985 - 1987. Direction: positive $\hat{Y}$ = easterly; negative $\hat{Y}$ = westerly.

Model 3. $\hat{Y} = 5.0087 + 0.7557X_1 + 0.0245X_2 - 0.0471X_3 - 0.0020X_4 - 0.0019X_5$

($R_a^2 = 0.328$; SE = 0.368; df = 5, 48; F = 6.1781; P < 0.001)

Where:

$\hat{Y}$ = Deviation of movement of collared animals from a north-south line. Only those days on which a proportion of the collared animals moved >1 SD of the $\bar{X}$ rate of travel (km·h-1) were used.

X_1, X_2, X_3, X_4, X_5 = Same as in original model.

R_a^2 > 0.1 and F > 2.0 (Appendix A). Comparison of these models (Appendix A) with the original model (Table 9; model 2) reveals their relative weakness; F values were less than half (2.81 vs. 6.04, respectively) and their significance levels were > 35 times that of the original model. Additionally, the adjusted multiple coefficients of determination were less than half that of the original model. Random data will produce significant models approximately 5% of the time (Wilkinson 1988, Snedecor and Cochran 1980), but the random models will seldom be as apt as models based upon real correlations (Wilkinson 1988), as demonstrated (Appendix A). Furthermore, random models were less likely to be selected because extensive comparison of partial models and similar models with other variables that were intercorrelated with those in the final model was done prior to selecting the final model. Independent variables, even when drawn from different models, complemented each other in determining weather conditions that resulted in movements different from average. Thus, the models presented were not likely to be based upon random correlations.

DISCUSSION

Separation of migration corridors (Fig. 4) as outlined in previous publications (Urquhart 1983, a review) is subject to question. Previous descriptions of the migration corridors were based upon repeated observations at irregular intervals of unmarked caribou. Frequent locations of satellite collared caribou (Fancy et al. 1988, 1989) suggest that routes used by caribou for autumn migration are not separate corridors, but rather part of a continuous corridor (Whitten and Fancy 1990) (Fig. 11). Entrances to the corridor are from the arctic coastal plain south through the Brooks Range and east along the coastal plain to the Barn Mountains in the northern Yukon Territory. The corridor then extends from the southern flanks of the Brooks Range through the Yukon Territory along the western edge of the Richardson Mountains, crosses the

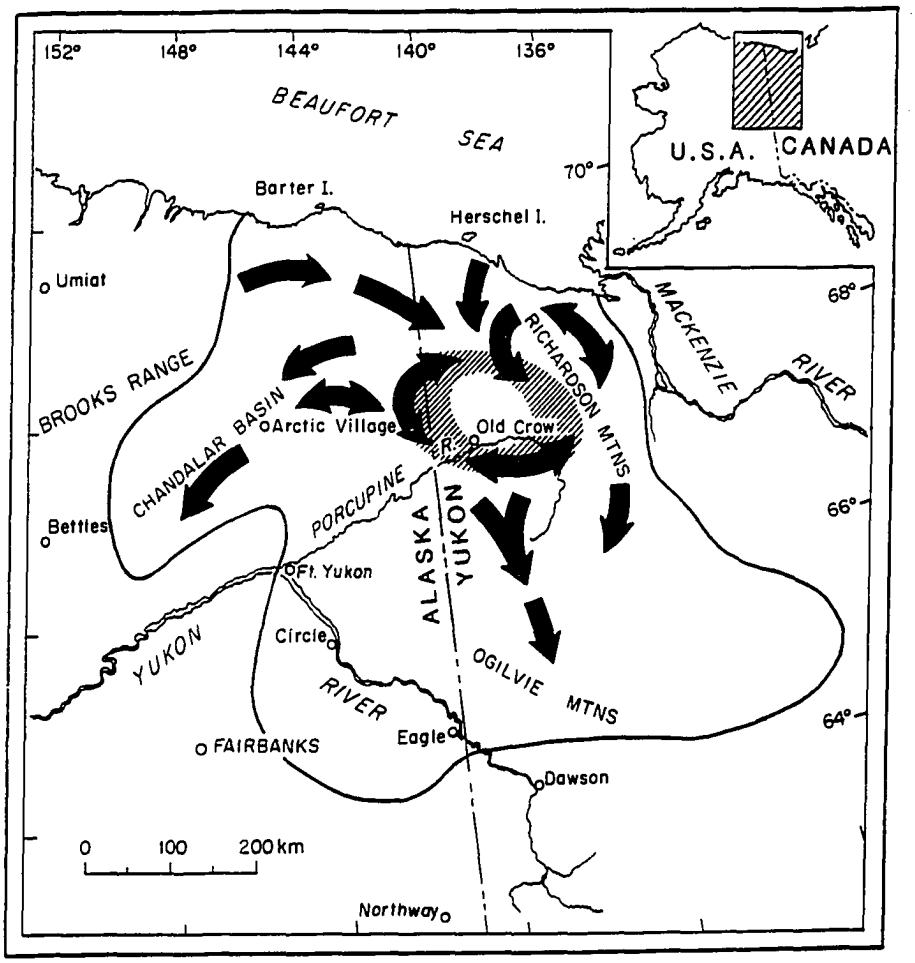

Figure 11. Schematic of autumn migration corridor used by satellite collared caribou for September and October, 1985 - 1989. (adapted from Whitten and Fancy 1990).

Porcupine River to the east of Old Crow, and passes north of the Ogilvie Mountains to the Porcupine River in eastern Alaska. The corridor circles north of the Porcupine River and north along the Alaska - Canada border back to the southern flanks of the Brooks Range. Caribou using the corridor leave at a point proximate to one of the wintering areas.

Relationships between weather and caribou movements are not simple (Appendix C) as indicated by the number of weather variables entering the multiple linear regression models. Variation in caribou movements is high (Figs. 5 - 10), but significance of the models ($P < 0.05$) (Tables 6, 8, 9, and 11) refutes the null hypothesis that weather does not influence the migration of PCH. Correlations between weather and movements are not consistent throughout each month. Variation in movements suggests that any models produced will be "noisy," but the low amount of overall variation in movements explained by the models ($R_a^2 < 0.41$) suggest that factors other than direct weather influence movement as well.

In September, caribou moved faster when the daily temperature flux was greater at Old Crow and Umiat, suggesting clear skies over the northern part of the PCH range, and when temperatures were lower at Bettles and Dawson. Larger changes in amount of daylight contribute toward the trend for increased movement, suggesting that weather conditions promoting increased movement may have a greater effect on caribou in the early part of that month. Weather variables that influenced directional movements in September were different from those that increased rates of movement. Easterly movements were fostered when the temperature flux was larger at Beaver Creek and smaller at Komakuk Beach, suggesting clear skies in the southern portion of the PCH range and cloudiness in the northern portion. These weather conditions had greater influence on September directional movements later during that month.

The relatively small amount of variation in rate of caribou movements explained by these models ($R_a^2 < 0.41$) calls to question the amount of direct influence that may be attributable to weather during

September. If the primary impetus is imparted to the autumn migration by early September storms (Banfield 1954a, 1954b; Kelsall 1968; Jakimchuk et al. 1974; McCourt et al. 1974; Roseneau et al. 1975; Surrendi and DeBock 1976; Thompson 1978; Ealey 1980), then >40% of the variation in movement should be explained by these models.

Direct influences of weather likely play an even smaller role in guiding east-west movements of the PCH in September ($R_a^2 = 0.16$; Table 8). Weather conditions that might influence east-west movements are not related ($P > 0.10$; Table 8) to those that increase rate of movement, because of the high variability of the directional model when applied only to days on which some proportion of the collared caribou moved >1 SD from the average (Table 8; Models 2 and 3).

Models for movement in September lend little support to Pendergast's (1973) assertion that caribou are predisposed to migrate by photoperiod. Photoperiod in September contributed less than any other variable toward explaining caribou rates of movement. I conclude that predisposition of PCH animals toward migration in early September must be small.

Photoperiod undoubtedly influences timing of reproduction (Bligh 1976, Budde 1983, Verme and Ozoga 1987). Daylength, mediated through the pineal gland, regulates melatonin production, which in turn influences timing of breeding (Adam and Atkinson 1984, Ryg 1986). This suggests that September pre-rut movements may be migratory restlessness, with the autumn migration actually beginning about the time of the onset of rut in late September and early October, as suggested for the Kaminuriak Herd (Parker 1972).

In October, caribou moved slower when there was more snow on the ground at Chandalar Lake early in that month. Caribou moved faster when daily temperature flux was higher at Barter Island and lower at Beaver Creek, suggesting clear skies to the north and cloudy skies to the south, and when precipitation was higher at Circle City. Weather had a greater influence on movement rates later in the month. PCH animals moved east

early in October when there was little snow falling or on the ground at Barter Island, and temperature flux was greater at Beaver Creek and lesser at Komakuk Beach.

The trend for decreased movement early in October (Table 9; model 1) is likely produced by rutting activity as well as a response to weather. This is further indicated by increased rates of movement later in October (Table 9; model 2) when traveling conditions presumably are poorer. Unlike September, weather factors involved in rate of movement are likely related to those correlated with direction of movement (Table 11; Models 2 and 3). The correlation of rate and direction of autumn migration of the PCH appears to take place coincident with the onset of rut in late September and early October. Peak calving of the PCH occurs June 3 - 5 (Garner and Reynolds 1986), and gestation of caribou is about 230 days (Skoog 1968); therefore peak rutting activity in the PCH occurs October 17 -19. Rutting activity typically starts 2 -3 weeks prior to peak rut, so the timing is the same as the correlation between rate and directional movement indicated by the models.

I suggest that weather parameters are not the proximate factor in autumn caribou migration, but rather may be the ultimate factor. Temperature, precipitation, and snowfall affect foraging conditions for caribou, as well as insect abundance, both of which would affect caribou rates and directions of movement.

Weather conditions would affect phenology and availability of vegetation, and thus foraging conditions for ungulates (Skoog 1968, Boertje 1984, Beier and McCullough 1990, Klein 1990). Lack of concurrence between rate and direction of movement in September can be explained by warmer temperatures and minimal snowfall that minimize plant senescence, including nutrient translocation to roots, and maintain moderate forage quality and high forage availability. In October, harsher conditions promote full dormancy in plants, and increase snow accumulation that reduce foraging opportunities for caribou (Boertje 1984). If patchy

distribution of forage in the landscape is the norm, caribou rapidly consume available forage and move on to the next area of good grazing.

Multiple linear regression models were built using only movements of collared female caribou, but autumn forage quality and quantity are critical for caribou of both sexes. Females lose weight during winter and the period of lactation (Reimers 1983b, Reimers et al. 1983, Skogland 1984). Within a month of parturition, females may regain some of the weight lost, but this compensatory regain is probably tempered by the level of harassment by insects in July and August (White et al. 1975, Russell 1976). Extended and severe insect harassment may contribute to severe weight loss through interruption of foraging and increased energy expenditures. Without sufficient weight gains prior to rut in late September and early October, female caribou may fail to conceive (Dauphiné 1976; R. D. Cameron, Alas. Dep. Fish and Game, unpubl. data).

Body condition of male caribou is at or near an annual low by late October. During rut, male ungulates reduce intake of forage and expend additional energy for rutting activities. For white-tailed deer (Odocoileus virginiana) (Ransom 1965), mule deer (Odocoileus hemionus) (Blood and Lovas 1966, Torbit et al. 1985), elk (Cervus elaphus) (Bubenik 1982), pronghorn (Antilocapra americana) (Bear 1971) and caribou (Dauphiné 1976), fat deposition usually reaches a peak prior to rut, after which fat for winter survival is regained to replace some of that lost during rutting activities. Thus, both sexes must maximize intake of nutritious forage prior to rut to maximize reproductive potential, and after rut to survive winter.

To maximize availability and quality of autumn forage, caribou track vegetation through its phenological stages (Klein 1970, 1982, 1990; Wright 1979). Rate of onset of plant dormancy in autumn ultimately is set by weather factors, but proximal factors in concert with plant physiological processes influence its timing (Miller 1976). Data on precipitation and

temperature included in the multiple linear regression models were measured on a regional scale and would affect the onset of dormancy in vegetation, but would be ameliorated or exacerbated by local features of habitat. Elevation, slope, aspect, distance from water, plant species and other factors, all influence the quality and quantity of forage produced and the phenological stage of the vegetation (Klein 1970, 1982, 1990).

Caribou are selective grazers and seek out plant species at different phenological states (Skoog 1968; Skogland 1972; Kuropat and Bryant 1980; White and Trudell 1980a, 1980b; White 1983; Boertje 1984; Kuropat 1984; Klein 1990). Forage quality and availability vary as a result of such factors as proximity to open water (Huot 1982), growing season in microhabitats (Miller 1976, Thing 1980), anti-herbivory compounds (Person et al. 1982), and others (Trudell et al. 1980). Forage availability and quality also are dependent upon plant distribution (Whitten and Cameron 1980). A plant growing in the northern part of its range may be affected by weather differently from one in the center or southern part of its distribution. Plant communities are composed of many species, some of which may be only marginally adapted to a specific locale, and onset of winter will affect each plant differently, resulting in a mosaic of phenological stages. Caribou, then, have a wide range of choices in which to forage during autumn migration and these choices are not always dictated by specific weather patterns.

Thus, the multiple linear regression models may reflect phenological tracking of forage by migrating caribou as well as direct effects of weather. Weather ultimately influences the vegetation, and therefore significance of the multiple linear regression models, but proximal factors make "noisy" models and reduce the predictability of the models. Paths chosen by migrating caribou may provide better foraging conditions at the time caribou choose them than alternate routes not chosen. Elk and deer migrations are primarily elevational rather than latitudinal (Wallmo and Regelin 1981, Adams 1982, Thomas and Irby 1990), but the pattern of

seeking out forage of high quality and biomass while migrating to winter ranges is well-documented in elk (Adams 1982) and deer (Wallmo and Regelin 1981, Beier and McCullough 1990, Thomas and Irby 1990). Caribou, then, probably migrate in the autumn along routes that provide better immediate foraging conditions than alternate routes and not directly toward desired wintering areas. Indeed, females show a lack of individual fidelity to winter range (S. G. Fancy, unpubl. data).

Factors other than vegetation may influence foraging conditions, such as harassment of caribou by insects in early September. Insects, particularly mosquitoes (Culicidae), biting midges (Ceratopogonidae), warble and bot flies (Oestridae) and others, harass caribou (White et al. 1975, Dau 1986), and affect their behavior and distribution north of the Brooks Range in summer (White et al. 1975, 1981; Curatolo 1975; Thomson 1977; Lawhead 1988). South of the Brooks Range, weather conditions conducive to insect activity persist longer into autumn and weather factors described by the models, mediated by smaller scale components such as aspect, elevation, and others, would all have an influence upon insect abundance (White et al. 1975, Dau 1986). South of the Brooks Range, mosquitoes and biting midges persist into September, albeit in relatively small numbers. These insects, and perhaps others, would alter foraging conditions for caribou, and thereby affect movements to avoid insects (White et al. 1975, 1981; Thomson 1977). Caribou reactions to insects likely would affect only early September movements when temperatures are warm.

Predation also would affect choice of foraging location by migrating caribou. Predation has been proposed as a primary factor in caribou selection of calving grounds (Bergerud et al. 1984, 1990; Bergerud and Page 1987), caribou selection of calving sites (Fancy and Whitten, in press), caribou population declines (Bergerud and Ballard 1988, 1989; but see Van Ballenberghe 1989), and caribou selection of wintering areas (Ferguson et al. 1988). Predator densities or the possibility of predator

presence may, then, have an influence on caribou selection of foraging locations during migration, and possibly upon specific pathways chosen in the broad migration route. Indeed, in the Serengeti ecosystem predators are known to affect the migratory behavior and selection of foraging sites by ungulates, but initiation of movements is driven by rain and subsequent forage development (Maddock 1979). The role of predation on caribou likely would not be greatly affected by autumn weather, but effects of predators on caribou movements could affect the models of movement.

CONCLUSIONS

Routes used by migrating caribou in autumn likely are not distinct, but rather part of a continuous corridor that connects summer and winter components of the range of the PCH. Weather conditions affect autumn migratory movements of the PCH, but the influence may be both direct and indirect. Weather conditions affect forage quality and quantity, as well as insect abundance, which in turn affect caribou movements. Other factors, such as predation, that are less likely to be affected by weather also may influence caribou movements.

Effects of photoperiod on the autumn PCH migration are not clear. Weather influences on caribou movements are more pronounced in early September and the relationship to photoperiod is weak, suggesting little predisposition to migrate related to photoperiod. Photoperiod effects, however, are much stronger in October, suggesting a link with rut. Rate and direction of movements are not linked in September, whereas October rates and directions of movement are related.

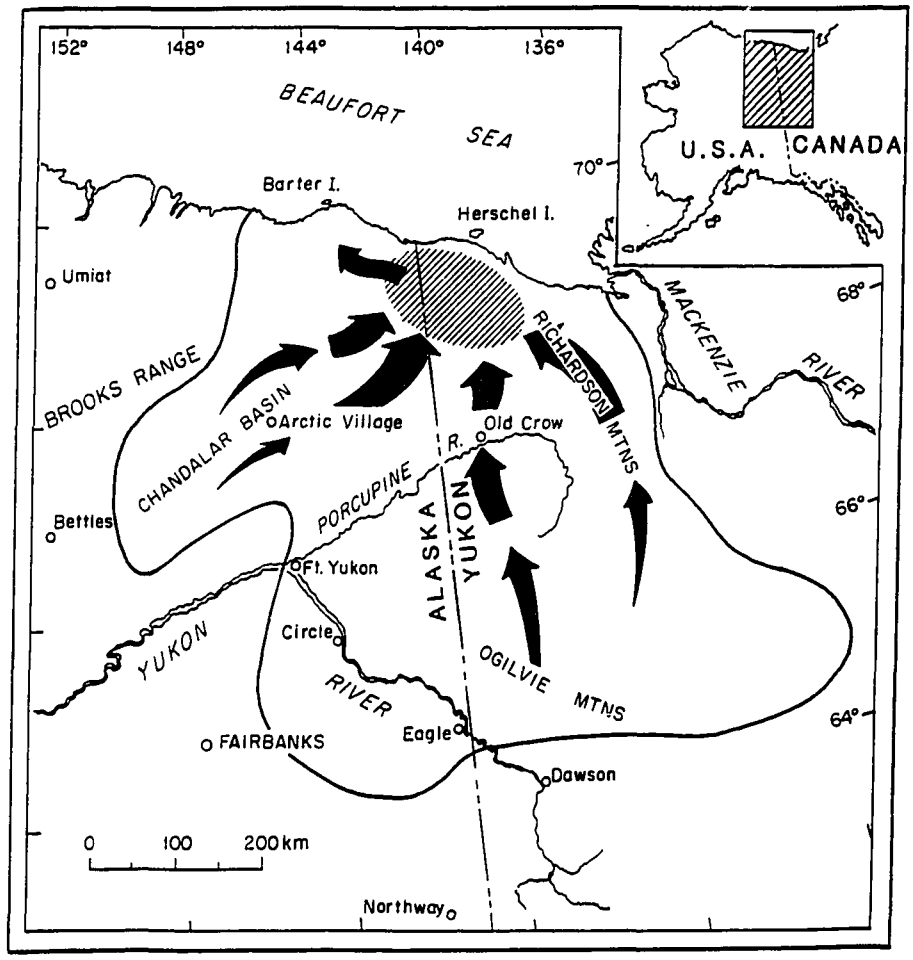

Figure 12. Wintering areas and spring migration routes of the PCH.

SPRING MIGRATION

INTRODUCTION

The consistent timing of spring migration argues for an internal motivation for migration modified by external factors (Geist 1971, Bergerud 1974); this is especially so for parturient females. Pregnant females must arrive on the calving grounds within a narrow time frame (Skoog 1968). Too early an arrival and caribou would have no forage, too late an arrival and forage would be past its peak nutritional status (Wright 1979, Boertje 1984, Eastland et al. 1989). Although motivated to migrate by hormonal changes associated with pregnancy (Bergerud 1974), timing of migration would be affected by traveling and foraging conditions (Bergerud 1974, Thompson 1978). Other caribou presumably migrate to enhance and extend range use as well as in response to other factors such as insect emergence and predators.

The Porcupine Caribou Herd has 3 main wintering areas (Figure 12), although caribou may winter in any portion of the total range in a particular year (Thompson 1978). The 3 wintering areas are the northern Richardson Mountains of the Yukon and Northwest Territories, the southern Richardson Mountains and Ogilvie Mountains of the Yukon Territory, and the Chandalar River basin of Alaska (Urquhart 1983). Caribou wintering in the Richardson Mountains usually migrate to the calving grounds on the arctic coastal plain by following the wind-swept ridges of the Richardsons, Barn and British mountains. Portions of the PCH wintering in the western Ogilvie Mountains usually migrate north along the Alaska - Canada border and those wintering in the eastern Ogilvies migrate north through the Richardsons. PCH animals wintering in the Chandalar area of Alaska migrate north and east along the southern flanks of the Brooks Range to

the British Mountains. All 3 migration corridors join in the British and Barn mountains, and caribou enter the coastal plain in the vicinity of the Blow and Babbage Rivers (Whitten and Fancy 1990; Fig. 7). Some animals wintering in the Chandalar area may migrate directly north through passes in the Brooks Range to the arctic coastal plain (Whitten and Cameron 1983).

Portions of the PCH wintering in the northern Richardson Mountains migrate the earliest, in late March or early April (Thompson 1978). Shallow snow on wind-swept ridges in the northern Richardson Mountains usually allow migration to begin as soon as females of the PCH are intrinsically ready (Skoog 1968, Jakimchuk and McCourt 1972, Bergerud 1974, McCourt et al. 1974, Hoffman 1975, Thompson 1978). Caribou wintering in the Ogilvie Mountains and the southern Richardsons often encounter deep snow that hinders movement (McCourt et al. 1974, Thompson 1978) and may not migrate until 1 month later (Thompson 1978). Caribou from the Chandalar winter range migrate in April and May (Duquette 1984). Spring migration ends in late May, or early June in years of heavy snowfall, when females arrive on the calving grounds.

Empirical evidence suggests that weather and snow factors are the primary influence on the timing of spring migration (Banfield 1954b, Pruitt 1959, Kelsall 1968, Lent 1966, Skoog 1968, McCourt et al. 1974, Roseneau and Stern 1974, Gavin 1975, Hoffman 1975, Roseneau et al. 1975, Thompson 1978, Duquette 1984). Thompson (1978) used temperature data from Ft. McPherson and Dawson City in the Yukon for a graphical analysis of spring migration timing for the years 1971 through 1974 and 1978. He reported that caribou migration along the Old Crow route and the second wave of caribou migration in the Richardson Mountains begins when the mean daily temperature at Dawson City reaches 4.4°C. This usually occurs in the first half of May (Thompson 1978:figs. 18-21), although it was about a month earlier in 1978 (Thompson 1978:fig. 22). Roseneau and Stern (1974) noted that initiation of spring migration by caribou wintering in

Alaska during winter 1971-72 coincided with rapid snowmelt because of daily temperatures >4°C on most days. Temperature is not thought to be the trigger for migration; it is merely an indicator of when snow depths will readily permit travel by caribou (Roseneau and Stern 1974, Thompson 1978). Hoffman (1975) documented that spring migration for part of the PCH wintering in the Richardson Mountains began immediately prior to a heavy snowfall. This documentation for a possible storm front effect could have been chance.

I used weather data from Alaska and Canada for the years 1986 - 1988 to test the hypothesis that weather is a major influence on the spring migration of the PCH. The null hypothesis would be that spring migration of the PCH is timed only to migratory urge -- a common date -- in most years.

METHODS

Data Collection

Weather data for April and May, 1986 - 1988, were obtained from 12 permanent weather stations within and near the range of the PCH. In Alaska, I obtained weather records for Barter Island, Bettles, Chandalar Lake, Circle City, Fort Yukon, Kuparuk, Northway, and Umiat (Natl. Oceanic and Atmos. Adm., Natl. Climatic Data Cent., Asheville, NC). Stations in Canada were located at Beaver Creek, Dawson City, Komakuk Beach, and Old Crow (Can. Climate Cent., Atmos. Environ. Serv., Downsview, Ontario, Can.) (Table 12). Weather and photoperiod variables used were the same as for my analyses of autumn migration. Wind was not used in the analyses because of differences in wind vectors at various altitudes and the effect of topography on ground-level winds. Wind would affect travel routes of caribou by blowing some ridges and slopes free of snow (Jakimchuk and McCourt 1974, McCourt et al. 1974, Hoffman 1975, Thompson 1978), but direction of wind likely would not be of importance in producing snow-free ridges.

Daily locations of female caribou were obtained using the Argos Data

Table 12. Location of weather stations that provided data used in the analyses of spring migration. Letters in parentheses are abbreviations used in text.

Station Name	North West Latitude	Longitude	Elevation (m)
Barter Island (BTI)[1]	70° 08′	143° 38′	13
Beaver Creek (BVR)[2]	62° 25′	140° 52′	649
Bettles (BTL)[1]	66° 55′	151° 31′	208
Chandalar Lake (CLK)[1]	67° 30′	148° 30′	595
Circle City (CCT)[1]	65° 50′	144° 04′	194
Dawson City (DAW)[2]	64° 03′	139° 08′	369
Fort Yukon (FYK)[1]	66° 33′	145° 12′	143
Komakuk Beach (KKK)[2]	69° 35′	140° 11′	7
Kuparuk (KPK)[1]	70° 19′	149° 35′	21
Northway (NTW)[1]	62° 58′	141° 56′	554
Old Crow (OLC)[2]	67° 35′	139° 50′	253
Umiat (UMT)[1]	69° 22′	152° 08′	86

[1]Alaska [2]Canada

Collection and Location System (Fancy et al. 1988) for March, April and May of 1986, 1987, and 1988. Small sample sizes in March precluded modeling as few collared caribou began migratory movements before April.

Data Analysis

I tested the influence of weather on spring migration of the PCH by multiple regression analyses. Rate and direction of movement were the dependent variables and were modeled as for my autumn analyses. Direction of movement was converted to sines to reflect west (sine = -1) and east (sine = 1) movement and cosines to reflect north (cosine = 1) and south (cosine = -1) movements and both directions of movement were modeled. Statistical procedures were identical to those described for autumn migration.

RESULTS

April

For April (Appendix C), apt models were built for movements >1 SD (Table 13; model 1) and >1.5 SD (Table 13; model 2) of the monthly mean ($\bar{X}$ = 0.2 km·h^{-1}, SD = 0.2). Sample sizes were inadequate to model movements >2 SD of the mean.

A significant trend ($R_a^2 \leq 0.315$, $p \leq 0.013$; Table 13) existed in April for caribou to move later in the month when the length of day was longer (DAYLONG): greatest rates of movement occurred later in the month (Table 14). Rates of movement were lower when difference between daily high and low temperature at Umiat (UMTCHGT) was large and precipitation was higher at Bettles, Beaver Creek, and Northway (BTLPPT, BVRPPT, and NTWPPT, respectively). Mean temperatures at Bettles, Beaver Creek, and Northway were -1.9, -1.7, and -1.6 °C, respectively, on dates when precipitation occurred, indicating that precipitation was heavy snow or mixed rain and snow. Increased snowfall at Barter Island (BTISF) also contributed to this trend, but BTISF was consistently <1 mm (Table 14). Standardized coefficients of regression (Table 13; models 1 and 2) indicated that none of the variables were of greater importance in

Table 13. Models for rate of movement in April, 1986 -1988.

Model 1. $\hat{Y} = -0.2589 + 0.0376X_1 - 0.0083X_2 - 0.0537X_3 - 0.0299X_4$

($R_a^2 = 0.194$; SE = 0.109; df = 4, 40; F = 3.648; P = 0.013)

Where:

$\hat{Y}$ = Proportion of the collared animals moving >1 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion > 0 were used.

X_1 = Length of day at 67° N, 141° W (DAYLONG)

X_2 = Difference between minimum and maximum temperature (°C) at Umiat, Alaska (UMTCHGT).

X_3 = Precipitation (mm) at Bettles, Alaska. Snow was melted prior to measurement (BTLPPT).

X_4 = Precipitation (mm) at Beaver Creek, Yukon Territory, Canada. Snow was melted prior to measurement (BVRPPT).

Variable	Standardized Coefficients
X_1 (DAYLONG)	0.2975
X_2 (UMTCHGT)	-0.2883
X_3 (BTLPPT)	-0.2852
X_4 (BVRPPT)	-0.3084

Table 13. (continued). Models for rate of movement in April, 1986 - 1988.

Model 2. $\hat{Y} = -0.5851 + 0.0459X_1 + 0.0544X_2 - 0.0332X_3$
($R_a^2 = 0.315$; SE = 0.076; df = 3, 25; F = 5.301; P = 0.006)

Where:

$\hat{Y}$ = Proportion of the collared animals moving >1.5 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion > 0 were used.

X_1 = Length of day at 67° N, 141° W (DAYLONG)

X_2 = Snowfall (mm) at Barter Island, Alaska (BTISF).

X_3 = Precipitation (mm) at Northway, Alaska. Snow was melted prior to measurement (NTWPPT).

Variable	Standardized Coefficients
X_1 (DAYLONG)	0.3226
X_2 (BTISF)	0.4585
X_3 (NTWPPT)	-0.5936

Table 14. Values of variables in models for April, 1986 - 1988.

Variable[1]	All days $\bar{X} \pm SD$ n = 90	Days on which at least 1 animal moved more than the specified SD above the average rate in $km \cdot h^{-1}$: 1 $\bar{X} \pm SD$ n = 45	1.5 $\bar{X} \pm SD$ n = 29
BTICHGT	9.4 ± 3.8	9.7 ± 4.2	9.0 ± 3.9
BTIMAXT	-15.0 ± 8.4	-10.4 ± 7.4	-8.1 ± 5.9
BTISF	0.6 ± 2.2	0.8 ± 2.7	0.3 ± 0.8
BTISOG	187 ± 100	172 ± 95	150 ± 83
BTLPPT	0.1 ± 0.6	0.1 ± 0.6	0.2 ± 0.8
BVRPPT	0.6 ± 2.2	0.4 ± 1.3	0.3 ± 1.0
CCTMAXT	0.0 ± 8.6	4.3 ± 7.0	7.1 ± 5.2
CLKPPT	0.0 ± 0.1	0.0 ± 0.1	0.0 ± 0.0
DAWPPT	0.5 ± 1.3	0.3 ± 0.9	0.4 ± 1.1
DAYLONG	15.6 ± 1.1	16.2 ± 1.0	16.6 ± 0.6
FYKPPT	0.0 ± 0.1	0.0 ± 0.2	0.0 ± 0.0
FYKSOG	220 ± 127	168 ± 138	137 ± 140
NTWMINT	-11.2 ± 8.1	-8.2 ± 6.8	-7.2 ± 4.9
NTWPPT	0.3 ± 1.0	0.3 ± 1.3	0.4 ± 1.6
UMTCHGT	13.1 ± 4.0	13.3 ± 4.2	12.7 ± 3.8

[1]DAYLONG = Day length in hours.

BTI = Barter Island
BTL = Bettles
BVR = Beaver Creek
CCT = Circle City
CLK = Chandalar Lake
DAW = Dawson City
FYK = Fort Yukon
NTW = Northway
UMT = Umiat

MAXT = Maximum daily temperature (°C).
MINT = Minimum daily temperature (°C).
CHGT = Difference between MINT and MAXT (°C).
PPT = Precipitation (mm) in water equivalent.
SF = Snowfall (mm).
SOG = Snow on ground (mm).

explaining the variation in caribou movements, although amounts of precipitation in the southern portion of the PCH range (NTWPPT, BVRPPT) contributed slightly more than other variables.

Caribou tended (R_a^2 = 0.182, p <0.001; Table 15) to move east in April when snow on ground at Barter Island (BTISOG), and Fort Yukon (FYKSOG) was deeper. Westerly movement occurred when temperature flux at Barter Island (BTICHGT) was greater, indicating clear skies in the north, and precipitation occurred at Chandalar Lake (CLKPPT) (Table 15). Mean temperature at Chandalar Lake was -8.6°C on days when precipitation occurred, so precipitation was probably snow. Standardized coefficients indicate that amount of snow on ground explained most variation in east - west movements (Table 15).

Northerly movements in April occurred (R_a^2 = 0.389, p < 0.001; Table 16) when maximum temperatures at Barter Island (BTIMAXT) and minimum temperatures at Northway (NTWMINT) were higher, and southerly movements occurred when precipitation was higher at Fort Yukon and Dawson City (FYKPPT, DAWPPT). Mean temperatures at Fort Yukon and Dawson for days on which precipitation occurred were -10.3 and -3.9 °C, respectively. Southerly movements also occurred when maximum temperatures at Circle City (CCTMAXT) were lower (Table 14). Temperature variables in the model explained most variation in north - south movements, demonstrated by the higher standardized coefficients of regression (Table 16).

May

Significant (P < 0.02) models were built for rate and direction of movement in May (Appendix C). Rate of movement ($R_a^2 \leq 0.354$, $p \leq 0.009$; Table 17) in May ($\bar{X}$ = 0.32 km·h^{-1}, SD = .28) was greater early in the month (JDAY). Timing of rate of movement, indicated by the first day of the month on which more than 1 animal moved >2 SD of the mean monthly rate, was different for April and May (t = 5.875, df = 2, P = 0.028). Higher average temperatures at Kuparuk (KPKAVGT: Table17; model 2) and Beaver Creek (BVRAVGT: Table 17; model 3) and precipitation at Northway

Table 15. Models for east-west deviation in movement during April, 1986 - 1988. Direction: positive $\hat{Y}$ = easterly; negative $\hat{Y}$ = westerly.

Model 1. $\hat{Y} = -0.3303 - 0.0115X_1 + 0.0009X_2 - 0.4206X_3 + 0.0009X_4$

($R_a^2 = 0.182$; SE = 0.267; df = 4, 85; F = 5.934; P < 0.001)

Where:

$\hat{Y}$ = Deviation of movement of collared animals from a north-south line.

X_1 = Difference between minimum and maximum temperature (°C) at Barter Island, Alaska (BTICHGT).

X_2 = Snow on ground (mm) at Barter Island, Alaska (BTISOG).

X_3 = Precipitation (mm) at Chandalar Lake, Alaska. Snow was melted prior to measurement (CLKPPT).

X_4 = Snow on ground (mm) at Fort Yukon, Alaska (FYKSOG).

Variable	Standardized Coefficients
X_1 (BTICHGT)	-0.1484
X_2 (BTISOG)	0.2927
X_3 (CLKPPT)	-0.1740
X_4 (FYKSOG)	0.4083

Table 16. Models for north-south deviation in movement during April, 1986 - 1988. Direction: positive $\hat{Y}$ = northerly; negative $\hat{Y}$ = southerly.

Model 1. $\hat{Y} = 0.7547 + 0.0233X_1 - 0.0129X_2 - 0.0484X_3 - 0.6492X_4 + 0.0142X_5$

($R_a^2 = 0.389$; SE=0.232; df=5, 84; F=12.328; P< 0.001)

Where:

$\hat{Y}$ = Deviation of movement of collared animals from an east-west line.

X_1 = Maximum temperature (°C) at Barter Island, Alaska (BTIMAXT).

X_2 = Maximum temperature (°C) at Circle City, Alaska (CCTMAXT).

X_3 = Precipitation (mm) at Dawson, Yukon Territory, Canada. Snow was melted prior to measurement (DAWPPT).

X_4 = Precipitation (mm) at Fort Yukon, Alaska. Snow was melted prior to measurement (FYKPPT).

X_5 = Minimum temperature (°C) at Northway, Alaska (NTWMINT).

Variable	Standardized Coefficients
X_1 (BTIMAXT)	0.6573
X_2 (CCTMAXT)	-0.3736
X_3 (DAWPPT)	-0.2195
X_4 (FYKPPT)	-0.2402
X_5 (NTWMINT)	0.3879

Table 17. Models for rate of movement in May, 1986 -1988.

Model 1. $\hat{Y} = 0.8894 + 0.1363X_1 - 0.0019X_2 - 0.0635X_3$

($R_a^2 = 0.350$; SE = 0.486; df = 3, 33; F = 7.466; P < 0.001)

Where:

$\hat{Y}$ = Proportion of the collared animals moving <1 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion >0 were used.

X_1 = Precipitation (mm) at Dawson, Yukon Territory. Snow was melted prior to measurement (DAWPPT).

X_2 = Snow on ground (mm) at Chandalar Lake, Alaska (CLKSOG).

X_3 = Minimum temperature (°C) at Barter Island, Alaska (BTIMINT).

Variable	Standardized Coefficients
X_1 (DAWPPT)	0.4307
X_2 (CLKSOG)	-0.4538
X_3 (BTIMINT)	-0.5843

Table 17 (continued). Models for rate of movement in May, 1986 - 1988.

Model 2. $\hat{Y} = 4.4097 - 0.0001X_1 + 0.0098X_2 - 0.0043X_3 + 0.0002X_4 - 0.0045X_5$

($R_a^2 = 0.222$; SE = 0.087; df = 5, 61; F = 4.762; P < 0.001)

Where:

$\hat{Y}$ = Proportion of the collared animals moving >1 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion >0 were used.

X_1 = Julian date (JDAY).

X_2 = Average temperature (°C) at Kuparuk, Alaska (KPKAVGT).

X_3 = Snowfall (mm) at Chandalar Lake, Alaska (CLKSF).

X_4 = Snow on ground (mm) at Chandalar Lake, Alaska (CLKSOG).

X_5 = Precipitation (mm) at Old Crow, Yukon Territory. Snow was melted prior to measurement (OLCPPT).

Variable	Standardized Coefficients
X_1 (JDAY)	-0.4071
X_2 (KPKAVGT)	0.3475
X_3 (CLKSF)	-0.2111
X_4 (CLKSOG)	0.2593
X_5 (OLCPPT)	-0.1715

Table 17 (continued). Models for rate of movement in May, 1986 -1988.

Model 3. $\hat{Y} = 3.6063 - 0.0001X_1 + 0.0126X_2 + 0.0073X_3 - 0.0252X_4$

($R_a^2 = 0.270$; SE = 0.060; df = 4, 42; F = 3.876; P = 0.009)

Where:

$\hat{Y}$ = Proportion of the collared animals moving >1.5 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion >0 were used.

X_1 = Julian date (JDAY).

X_2 = Average temperature (°C) at Beaver Creek, Yukon Territory (BVRAVGT).

X_3 = Precipitation (mm) at Northway, Alaska. Snow was melted prior to measurement (NTWPPT).

X_4 = Precipitation (mm) at Old Crow, Yukon Territory. Snow was melted prior to measurement (OLCPPT).

Variable	Standardized Coefficients
X_1 (JDAY)	-0.5047
X_2 (BVRAVGT)	0.4161
X_3 (NTWPPT)	0.3947
X_4 (OLCPPT)	-0.3135

Table 17 (continued). Models for rate of movement in May, 1986 -1988.

Model 4. $\hat{Y} = 0.0943 + 0.0072X_1 - 0.1757X_2 + 0.0006X_3$
($R_a^2 = 0.354$; SE = 0.049; df = 3, 30; F = 7.024; P = 0.001)

Where:

$\hat{Y}$ = Proportion of the collared animals moving >2 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion >0 were used.

X_1 = Difference (°C) between daily high and low temperature at Komakuk Beach, Yukon Territory (KKKCHGT).

X_2 = Precipitation at Barter Island, Alaska. Snow was melted prior to measurement (BTIPPT).

X_3 = Snow on ground (mm) at Bettles, Alaska (BTLSOG).

Variable	Standardized Coefficients
X_1 (KKKCHGT)	0.3607
X_2 (BTIPPT)	-0.3500
X_3 (BTLSOG)	0.4465

(NTWPPT: Table 17; model 3) were correlated with increased rates of movement, while precipitation at Dawson City (DAWPPT: Table 17; model 1), Old Crow (OLCPPT: Table 17; models 2, 3), and Barter Island (BTIPPT: Table 17; model 4) were correlated with decreased rates of movement. Snow on ground at Chandalar Lake (CLKSOG: Table 17; models 1, 2) and Bettles (BTLSOG: Table 17; model 4) were correlated with increased rates of movement, but depths were not great (<14 cm, Table 18) and additional snowfall at Chandalar Lake (CLKSF: Table 17; model 2) decreased movement. Colder minimum temperatures at Barter Island (BTIMINT: Table 17; model 1) increased movement as did larger differences between daily high and low temperatures at Komakuk Beach (KKKCHGT: Table 17; model 4). Standardized coefficients of regression indicate that precipitation and snowfall variables contributed less to the multiple linear regression models of rate of movement than did Julian date (timing of movements), temperature, and snow on ground (Table 17).

Northerly movements in May ($R_a^2 = 0.420$, $p < 0.001$; Table 19) were early in the month when change in daylight from the previous day (DAYCHG) was less. Precipitation at Barter Island (BTIPPT) and Bettles (BTLPPT) was correlated with northerly movements while precipitation at Old Crow (OLCPPT) decreased such movements. Snow on ground at Umiat (UMTSOG) minimized northerly movement. Snow on ground at Bettles (BTLSOG) increased northerly movement, but additional snowfall at Bettles (BTLSF) decreased northerly movements. Snow on ground at Umiat averaged 340 mm for May while BTLSOG was only 11 mm (Table 18). Cooler mean temperatures at Northway (NTWAVGT) increased northerly movements. DAYCHG and NTWAVGT contributed the most to the multiple linear regression model for north - south movements and precipitation variables contributed the least (Table 19).

East - west movements ($R_a^2 = 0.573$, $p < 0.001$; Table 20), like north - south movements, were greater early in May (JDAY). The mean date for movements >2 SD to begin was 17 April versus 2 May. Greater snow on ground

Table 18. Values of variables in models for May, 1986 - 1988.

Variable[1]	All days $\bar{X} \pm SD$ n = 93	Days on which movements of at least 1 animal differed by the specified SD of the mean rate in $km \cdot h^{-1}$	
		-1 $\bar{X} \pm SD$ n = 37	+1 $\bar{X} \pm SD$ n = 67
BTIMINT	-9.4 ± 4.9	-10.0 ± 5.5	-8.6 ± 4.2
BTIPPT	0.1 ± 0.3	0.1 ± 0.1	0.1 ± 0.1
BTLPPT	0.7 ± 2.0	1.0 ± 2.4	0.7 ± 2.0
BTLSOG	11 ± 32	7 ± 16	13 ± 37
BTLSF	1.1 ± 7.5	1.8 ± 10.9	0.5 ± 3.7
BVRAVGT	5.9 ± 2.4	5.6 ± 2.1	5.5 ± 2.2
CLKPPT	0.6 ± 2.2	0.5 ± 2.3	0.5 ± 1.8
CLKSF	1.7 ± 11.3	0.0 ± 0.1	0.8 ± 4.9
CLKSOG	108 ± 145	119 ± 142	116 ± 147
DAWPPT	1.1 ± 2.6	1.0 ± 1.9	1.3 ± 3.0
DAWSF	0.6 ± 4.2	0.8 ± 4.8	0.4 ± 3.5
DAYCHG	10.0 ± 2.3	10.0 ± 2.6	9.7 ± 2.0
FYKPPT	0.2 ± 1.0	0.0 ± 0.1	0.2 ± 1.1
KKKCHGT	6.2 ± 3.2	5.9 ± 3.5	6.5 ± 3.4
KPKAVGT	-7.3 ± 4.0	-7.6 ± 4.3	-6.9 ± 3.5
NTWAVGT	7.2 ± 2.9	7.1 ± 2.8	6.9 ± 2.8
NTWPPT	1.5 ± 3.4	1.6 ± 4.1	1.4 ± 3.4
OLCMINT	-4.5 ± 5.5	-5.5 ± 5.5	-4.0 ± 5.2
OLCPPT	0.7 ± 3.6	0.6 ± 2.8	0.6 ± 3.7
UMTSOG	340 ± 155	375 ± 132	345 ± 142

Table 18 (continued). Values of variables in models for May, 1986 - 1988.

Variable[1]	Days on which at least 1 animal moved more than the specified SD above the average rate in $km \cdot h^{-1}$	
	+1.5 $\bar{X} \pm SD$ n = 47	+2 $\bar{X} \pm SD$ n = 34
BTIMINT	-8.8 ± 4.6	-8.3 ± 4.6
BTIPPT	0.1 ± 0.1	0.1 ± 0.1
BTLPPT	0.6 ± 1.7	0.3 ± 0.8
BTLSOG	17 ± 42	15 ± 44
BTLSF	0.0 ± 0.1	0.0 ± 0.1
BVRAVGT	5.4 ± 2.2	5.4 ± 2.0
CLKPPT	0.6 ± 2.1	0.4 ± 1.1
CLKSF	1.1 ± 5.8	1.5 ± 6.8
CLKSOG	138 ± 157	131 ± 161
DAWPPT	0.9 ± 2.1	1.1 ± 2.3
DAWSF	0.6 ± 4.2	0.8 ± 5.0
DAYCHG	9.4 ± 1.9	9.6 ± 1.8
FYKPPT	0.3 ± 1.3	0.4 ± 1.5
KKKCHGT	6.3 ± 3.1	6.2 ± 3.1
KPKAVGT	-7.1 ± 3.7	-6.7 ± 3.7
NTWAVGT	6.7 ± 2.8	6.7 ± 2.5
NTWPPT	1.4 ± 3.6	1.9 ± 4.2
OLCMINT	-4.0 ± 5.4	-4.0 ± 5.4

Table 18 (continued). Values of variables for May.

OLCPPT	0.3 ± 0.8	0.3 ± 1.0
UMTSOG	342 ± 139	329 ± 135

[1]DAYCHG = Change in daylight from the previous day in minutes and decimal minutes.

BTI = Barter Island
BTL = Bettles
BVR = Beaver Creek
CLK = Chandalar Lake
DAW = Dawson City
FYK = Fort Yukon
KKK = Komakuk Beach
KPK = Kuparuk
NTW = Northway
OLC = Old Crow
UMT = Umiat

AVGT = Average daily temperature (°C).
MINT = Minimum daily temperature (°C).
CHGT = Difference (°C) between minimum and maximum daily temperature.
PPT = Precipitation (mm) in water equivalent.
SF = Snowfall (mm).
SOG = Snow on ground (mm).

Table 19. Models for north-south deviation in movement during May, 1986 - 1988. Direction: positive $\hat{Y}$ = northerly; negative $\hat{Y}$ = southerly.

Model 1. $\hat{Y} = 1.0993 - 0.0422X_1 - 0.0285X_2 + 0.0918X_3 + 0.0173X_4 - 0.0094X_5 + 0.0013X_6 - 0.0100X_7 - 0.0004X_8$

($R_a^2 = 0.420$; SE = 0.171; df = 7, 85; F = 9.339; P < 0.001)

Where:

$\hat{Y}$ = Deviation of movement of collared animals from an east-west line.

X_1 = Change in length of day (min) from previous day at 67° N, 141° W (DAYCHG).

X_2 = Average temperature (°C) at Northway, Alaska (NTWAVGT).

X_3 = Precipitation (mm) at Barter Island, Alaska. Snow was melted prior to measurement (BTIPPT).

X_4 = Precipitation (mm) at Bettles, Alaska. Snow was melted prior to measurement (BTLPPT).

X_5 = Snowfall (mm) at Bettles, Alaska (BTLSF).

X_6 = Snow on ground (mm) at Bettles, Alaska (BTLSOG).

X_7 = Precipitation (mm) at Old Crow, Yukon Territory. Snow was melted prior to measurement (OLCPPT).

X_8 = Snow on ground at Umiat, Alaska (UMTSOG).

Table 19 (continued). Models for north-south deviation in movement May, 1986 - 1988. Direction: positive $\hat{Y}$ = northerly; negative $\hat{Y}$ = southerly.

Variable	Standardized Coefficients
X_1 (DAYCHG)	-0.4240
X_2 (NTWAVGT)	-0.3652
X_3 (BTIPPT)	0.1230
X_4 (BTLPPT)	0.1527
X_5 (BTLSF)	-0.3140
X_6 (BTLSOG)	0.1949
X_7 (OLCPPT)	-0.1608
X_8 (UMTSOG)	-0.2833

at Bettles (BTLSOG) and Umiat (UMTSOG) contributed to westerly movement, while snow on ground at Chandalar Lake (CLKSOG) decreased westerly movement. Increased precipitation at Chandalar Lake (CLKPPT) and Fort Yukon (FYKPPT) fostered westerly movement as did snowfall at Dawson City (DAWSF)and cooler minimum temperatures at Old Crow (OLCMINT). As with north - south movement, timing of movements (JDAY) contributed most to the multiple linear regression model, indicated by the standardized coefficients (Table 20). CLKSOG and UMTSOG contributed more to the explanation of variation in east - west movements than did BTLSOG, and precipitation variables contributed relatively little (Table 20).

DISCUSSION

Timing of migration reflected in my models indicate that most coordinated movements occurred in late April and early May for 1986 - 1988 (Appendix C). Migratory movements of the PCH can begin as early as March (McCourt et al. 1974), but they mainly occur in April and May (Jakimchuk et al. 1974, McCourt et al. 1974, Roseneau and Curatolo 1975, Roseneau et al. 1975, Thompson 1978, Whitten and Cameron 1983, Duquette 1984).

Females are suggested to be intrinsically prepared to migrate to the calving grounds in the spring by photoperiod and hormonal changes associated with pregnancy (Skoog 1968, Bergerud 1974). Timing, however, is not the sole factor in influencing spring migration of the PCH (Tables 13, 17, 19, and 20). Weather variables exert greater influence on rate of movement than timing in April (Table 13), and strongly influence all movements in May (Tables 17, 19, and 20). The influence of weather variables suggests that the intrinsic drive to reach the calving grounds probably increases with time (Bergerud 1974), so snow conditions that hinder movement in April might not do so in May (Pruitt 1959).

The initial migratory urge in females, manifested by coordinated directional movements, may well be caused by intrinsic factors (Skoog 1968, Geist 1971, Bergerud 1974), but migration occurs when snow conditions permit (Banfield 1954a, Pruitt 1959, Kelsall 1968, Skoog 1968,

Table 20. Models for east-west deviation in movement during May, 1986 - 1988. Direction: positive $\hat{Y}$ = easterly; negative $\hat{Y}$ = westerly.

Model 1. $\hat{Y} = 29.9147 - 0.0003X_1 - 0.0347X_2 - 0.00032X_3 - 0.0214X_4 + 0.0014X_5 - 0.0157X_6 - 0.0772X_7 - 0.0018X_8$

($R_a^2 = 0.573$; SE = 0.259; df = 8, 84; F = 16.419; P < 0.001)

Where:

$\hat{Y}$ = Deviation of movement of collared animals from a north-south line.

X_1 = Julian date (JDAY).

X_2 = Minimum temperature (°C) at Old Crow, Yukon Territory (OLCMINT).

X_3 = Snow on ground (mm) at Bettles, Alaska (BTLSOG).

X_4 = Precipitation (mm) at Chandalar Lake, Alaska. Snow was melted prior to measurement (CLKPPT).

X_5 = Snow on ground (mm) at Chandalar Lake, Alaska (CLKSOG).

X_6 = Snowfall (mm) at Dawson, Yukon Territory (DAWSF).

X_7 = Precipitation (mm) at Fort Yukon, Alaska (FYKPPT).

X_8 = Snow on ground at Umiat, Alaska (UMTSOG).

Variable	Standardized Coefficients
X_1 (JDAY)	-0.7017
X_2 (OLCMINT)	-0.4797
X_3 (BTLSOG)	-0.2671
X_4 (CLKPPT)	-0.1206
X_5 (CLKSOG)	0.5020
X_6 (DAWSF)	-0.1640
X_7 (FYKPPT)	-0.1923
X_8 (UMTSOG)	-0.6978

Gavin 1975), usually in April and May (Thompson 1978). Significance ($p \leq 0.013$) of the models and variables selected by the multiple linear regression procedures support this view. Unlike autumn migration, spring migration has a definite endpoint: the calving grounds (Skoog 1968). Thus, female caribou have both a place to which they are going and a time by when they attempt to arrive to give birth. Amounts of variation in movements explained by the models ($R_a^2 \leq 0.573$) may be attributed to the variation in caribou behavior under different snow conditions.

Weather influences ($p \leq 0.013$) both rate and direction of movement of spring migration of the PCH. Observations of unmarked animals, has led to the contention that the primary influence on spring migration of caribou has been snow conditions (Banfield 1954a, Pruitt 1959, Kelsall 1968, Skoog 1968, Parker 1972, Hoffman 1975, Roseneau and Curatolo 1976, Surrendi and DeBock 1976, Thompson 1978, Duquette 1984, Garner and Reynolds 1986). Weather variables for the multiple linear regression models selected by true-stepping and all-possible-regressions are all related to snow conditions and thus support this hypothesis.

Thompson (1978) used temperature data from Dawson City, Yukon Territory and movements of unmarked caribou to predict timing of the spring migration. He suggested that spring migration would occur when mean daily temperature at Dawson City was 4.4°C. Thompson (1978) states that "significant reductions in snow cover would be occurring" concurrently with the 4.4°C temperature at Dawson City. Variables in the models do support the notion that snow conditions are related to the timing of spring migration in the PCH.

For both April and May, similarity in the variables among models strongly suggests that both rate and direction of movement are related. Temperature and precipitation, variables that repeatedly occurred in the models, affect snow conditions which in turn affect caribou (Pruitt 1959). Snow density and hardness typically increase at higher snow temperatures (Gold 1956, Coady 1974) and fluctuations in temperature during winter

cause crusts to develop throughout the snow layer (Pruitt 1959). Pruitt (1959) noted that caribou moved from areas of greater snow depth and hardness to areas of lesser hardness and depth. He also observed that caribou tolerance of snow hardness varied, perhaps associated with tolerance to snow characteristics developed over winter. Multiple linear regression models indicated that cold temperatures retarded movement and additional snow either retarded movement or initiated movement, apparently to avoid areas of snowfall.

As snow depths approach brisket height, the energetic cost of locomotion increases greatly (Parker et al. 1984, Fancy 1986, Fancy and White 1987, Dailey and Hobbs 1989). Layers of crust within snow also affect efficiency of locomotion, but location and hardness of crusts determine effects upon caribou. Crusts in the upper layers of snow appear to hinder caribou movements more than crusts in lower layers (Pruitt 1959). Crusts hard enough to support caribou decrease the energetic cost of locomotion, whereas crusts that provide resistance to walking caribou but break under the weight of the animal increase energetic costs (Fancy 1986, Fancy and White 1987). Values for snow on ground in multiple linear regressions were well below caribou brisket height (51 - 72 cm, Fancy 1986) (Tables 14 and 18), indicating that snow hardness and density, reflected in the temperature and precipitation variables, exerted the greater influence on caribou movements for conditions occurring during my study.

Caribou also have a direct affect upon the snow conditions by trail breaking activities (Duquette 1984, Duquette and Klein 1987) that pack snow and increase snow hardness, thereby greatly reducing energy expenditures while traveling (Duquette 1984, Fancy 1986). Thus, caribou activities change the way they respond to particular snow conditions and decrease the variation in movements explained by the models. Additional decreases in the explanatory power of model variables likely occur from caribou choices of travel routes. Ridgelines and high places may be blown

free of snow and provide lanes of easier traveling (Jakimchuk and McCourt 1972, McCourt et al. 1974, Hoffman 1975, Thompson 1978), even though snow depths in surrounding valleys would hinder movements.

Snow conditions also affect foraging conditions for migrating caribou (Pruitt 1959, Bergerud 1971, Duquette 1984, Fancy 1986, Duquette and Klein 1987, Duquette 1988, Fleischman 1990). Energetic costs of cratering for forage increase with snow hardness (Fancy and White 1985, Fancy 1986, Fleischman 1990). Pruitt (1959) noted that caribou fed in previously cratered areas a second time, but not more frquently, presumably because disturbances to snow cover increase hardness beyond the point at which energy expenditures exceed the nutrition gained. Lightly crusted snow, which results from higher temperatures, may take less time for caribou to crater (Fleischman 1990), thus reducing overall energy expenditure. Nonetheless, energy expended by cratering caribou is small in all but the most heavily crusted snow when compared to the costs of locomotion (Fancy and White 1985, Fancy 1986).

CONCLUSIONS

Spring migration of the PCH is, in contrast to the autumn migration, a directed movement with a definite endpoint: the calving grounds on the Arctic coastal plain. Prevailing thought is that female caribou are intrinsically ready to initiate spring migration, but are restrained by snow conditions that affect both traveling and foraging conditions. Multiple linear regression models of caribou movements and weather in and near the range of the PCH support this view of caribou ecology.

SUMMARY

Selection of calving sites

In contrast to suggestions that caribou calve in areas free of snow (Lent 1980), calving sites with >75% snowcover were selected by caribou on the arctic coastal plain from 1974 to 1987 more often than zones with <25% snowcover for concentrated calving activity (Tables 2 and 3; $G = 7.703$, df = 2, $P = 0.02$). Post-parturient caribou thereby derived several benefits from the dynamics of snowmelt. I postulate that extended time of access to high-quality forage allowed females to minimize weight losses to maintain physiological condition (Rognmo et al. 1983; White and Luick 1984) for future reproduction (Thomas 1982, Reimers 1983a, White 1983, Tyler 1987, R. D. Cameron, AK Dept. Fish and Game, unpubl. data) while meeting lactational demands. Minimized weight losses during lactation coupled with weight gains after the period of peak lactation should allow females to maximize their body condition and their chances for conception at rut. Calves also were in areas with reduced densities of predators and were cryptically concealed within snowmelt patches from predators. Thus, it is likely that both nutrition and predator avoidance are responsible for site selection within the overall calving grounds.

Autumn migration

In contrast to earlier descriptions of the autumn migration corridors of the PCH McCourt et al. 1974, Roseneau and Stern 1974, Surrendi and DeBock 1976, Thompson 1978, Whitten and Cameron 1983) (Fig. 3), recent satellite telemetry results (Whitten and Fancy 1990) indicate that routes used by migrating caribou in autumn likely are not distinct, but rather part of a continuous corridor that connects summer and winter components of the range of the PCH (Fig. 11).

Parker (1972) noted that September movements in the Kaminuriak Herd

were considered to be part of the summer dispersal and did not consider true migratory movements to begin until October, and results of my models indicate a similar pattern for the PCH. Rate and direction of movements were not linked in September ($p > 0.10$) (Table 8, models 2 and 3), suggesting that September movements were a form of migratory restlessness, whereas October rates and directions of movement were related ($p < 0.001$) (Table 11, models 2 and 3), implying that caribou were moving in a coordinated, directional manner normally associated with migratory movements.

Pendergast (1973) hypothesized that PCH animals are predisposed to migrate in September by photoperiod. Effects of photoperiod on the autumn PCH migration were not uniform for September (Tables 6 and 8) and October (Tables 9 and 11). Weather influences on caribou movements were more pronounced in early September and the relationship to photoperiod was weak (Tables 6 and 8), suggesting little predisposition to migrate related to photoperiod in September. Photoperiod effects, however, were much stronger in October (Tables 9 and 11), indicating a strong link with rut. If, as I suggest, autumn migration of the PCH begins with the onset of rut in late September and early October, then photoperiod likely influences the initiation of migration, but it does not appear greatly to influence movements in September.

Weather conditions affected both rate (Tables 6 and 9) and direction (Tables 8 and 11) of autumn migratory movements ($p < 0.05$) of the Porcupine Caribou Herd, but the influence may be indirect ($R_a^2 < 0.41$). Weather conditions affect forage quality and quantity, as well as insect abundance. Because both affect caribou movements throughout summer and autumn, they jointly may have a stochastic effect on individual caribou locations in relation to the overall migration corridor and correlation with timing and direction of movement is therefore less precise. This is especially so when other factors, such as predation, that are less likely to be affected by weather also may influence caribou movements.

Weather factors influence autumn migration of the PCH ($p < 0.05$), but I suggest that weather is more an ultimate rather than proximate influence. The requirement for both sexes to maximize body condition for reproduction and winter survival (Dauphiné 1976, Thomas 1982, Reimers 1983a, White 1983, Tyler 1987) suggests that nutrition, directly related to forage quality, and forage availability likely are proximate factors influencing autumn migration early movements. In warm Septembers insect harassment also may influence foraging conditions. These proximate factors are not necessarily related to immediate weather conditions but rather may be a product of cumulative weather patterns and thus the lack of explanatory power of the models developed by this study. Movements by caribou to avoid predators would not be related to weather and such movements would increase the variation in caribou movements and further reduce the explanatory power of the models.

Spring migration

The spring migration of females of the PCH is, in contrast to the autumn migration, a directed movement with a fairly defined initiation combined with a definite endpoint: calving grounds on the arctic coastal plain. Prevailing thought is that female caribou are intrinsically ready to initiate spring migration in the last stage of pregnancy (Skoog 1968, Bergerud 1974), but are restrained by snow conditions that affect both traveling and foraging conditions.

The timing of initiation of spring migration suggested by my multiple linear regression models of caribou movements indicated that initiation of spring migration began in late April (Table 13) and early May (Table 17), although spring migration has been reported as early as March (Thompson 1978). Rate and direction of movement were related for both April (Tables 13, 15, 16) and May (Tables 17, 19, 20). Variables selected by the multiple regression model building process supported the idea that spring migration of females is driven by timing but that they

are braked by snow conditions that influence traveling and foraging.

Conclusions

My results support the hypothesis that migratory animals must redistribute themselves prior to the period of resource shortage for optimal use of habitats (Geist 1971). Autumn migration was a two-stage process beginning in September with pre-rut movements south of the Brooks Range providing caribou access to late summer forage while weather conditions are mild enough to provide minimal impediments to travel. Caribou then avoid the increasingly harsh conditions north of the Brooks Range and are adjacent to winter ranges. With the onset of rut in early October, movements are coordinated in both direction and rate of travel and are thus true migratory movements that end on the wintering area.

My examination of spring migrations and selection of calving sites suggests a corollary to the hypothesis of animal redistribution: animals must occupy a habitat prior to the period of resource abundance in that habitat. Porcupine Caribou Herd females in most years move from wintering areas to the coastal plain prior to the first flush of vegetation on the calving grounds. The spring migration must be completed prior to calving else the new-born offspring would delay migration for at least 3 weeks. By carrying the fetuses to calving sites on spring ranges, females forego early greening vegetation south of the Brooks Range but have access to nutritious forage immediately upon availability.

This study was not designed, nor was it able, to evaluate specific vegetation characteristics that enhance foraging for caribou in the autumn. Previous studies of forage for caribou concentrated on periods when phenological change in vegetation was relatively stable; i.e., in summer and winter. Weather variables in my models suggest that phenology of vegetation during times of rapid change (i.e., spring and autumn) are of importance to maintenance of caribou body condition and influence the movement and migration of caribou.

The models I developed indicate that immediate weather conditions

are an ultimate rather than a proximate influence on caribou migration. Further studies on proximate factors such as vegetation and snow conditions likely would produce data for models with greater explanatory power and predictability of caribou movements than those built by this study.

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Appendix A

Table 21. Models for rate of movement in October, 1985-1987, with randomly generated data substituting for actual data for the independent variables.

Model 1. $\hat{Y} = 0.7762 - 0.0505X_1 + 0.0004X_2 + 0.0054X_3 - 0.0084X_4$

($R_a^2 = 0.108$; SE = 0.174; df = 4, 48; F = 2.57; P = 0.05)

Where:

$\hat{Y}$ = Proportion of the collared animals moving > 1 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion > 0 were used (actual data).

X_1 = Length of day at 67° N, 141° W (DAYLONG)[a].

X_2 = Difference (°C) between minimum and maximum daily temperatures at Beaver Creek, Yukon Territory for the day on which movement occurred (BVRCHGT)[a].

X_3 = Amount of daily precipitation (mm) at Circle City, Alaska. Snow was melted prior to measurement (CCTPPT)[a].

X_4 = Difference (°C) between daily minimum and maximum temperatures at Barter Island, Alaska (BTICHGT)[a].

Variable	Standardized Coefficients
X_1 (DAYLONG)[a]	-0.401
X_2 (BVRCHGT)[a]	0.013
X_3 (CCTPPT)[a]	0.196
X_4 (BTICHGT)[a]	-0.151

[a]Randomly generated data.

Table 21. (continued)

Model 2. $\hat{Y} = 0.8735 - 0.0406X_1 - 0.0053X_2 - 0.0041X_3 - 0.0107X_4$

($R_a^2 = 0.122$; SE = 0.173; df = 4, 48; F = 2.81; P = 0.035)

Where:

$\hat{Y}$ = Proportion of the collared animals moving > 1 SD of the $\bar{X}$ rate of travel ($km \cdot h^{-1}$). Only those days on which proportion > 0 were used (actual data).

X_1 = Length of day at 67° N, 141° W (DAYLONG)[a].

X_2 = Difference (°C) between minimum and maximum daily temperatures at Beaver Creek, Yukon Territory for the day on which movement occurred (BVRCHGT)[a].

X_3 = Amount of daily precipitation (mm) at Circle City, Alaska. Snow was melted prior to measurement (CCTPPT)[a].

X_4 = Difference (°C) between daily minimum and maximum temperatures at Barter Island, Alaska (BTICHGT)[a].

Variable	Standardized Coefficients
X_1 (DAYLONG)[a]	-0.318
X_2 (BVRCHGT)[a]	-0.179
X_3 (CCTPPT)[a]	-0.148
X_4 (BTICHGT)[a]	-0.211

[a]Randomly generated data.

Appendix B

Table 22. Pearson correlation matrix for variables in models for September.

	DAYLONG	DAYCHG	BTIMINT	BTLAVGT	BVRCHGT
DAYLONG	1.00				
DAYCHG	0.92	1.00			
BTIMINT	0.70	0.57	1.00		
BTLAVGT	0.59	0.51	0.67	1.00	
BVRCHGT	0.13	0.11	0.31	0.39	1.00
DAWAVGT	0.61	0.52	0.66	0.64	0.19
DAWMINT	0.35	0.27	0.36	0.27	-0.31
KKKCHGT	0.10	0.09	0.09	0.25	0.41
OLCCHGT	0.19	0.16	0.22	0.42	0.58
UMTCHGT	0.18	0.16	0.04	0.20	0.34
UMTMAXT	0.67	0.59	0.73	0.76	0.48

	DAWAVGT	DAWMINT	KKKCHGT	OLCCHGT	UMTCHGT
DAWAVGT	1.00				
DAWMINT	0.80	1.00			
KKKCHGT	0.03	-0.24	1.00		
OLCCHGT	0.15	-0.25	0.54	1.00	
UMTCHGT	0.02	-0.19	0.47	0.44	1.00
UMTMAXT	0.52	0.11	0.46	0.47	0.57

	UMTMAXT
UMTMAXT	1.00

Table 23. Pearson correlation matrix for variables in models for October.

	DAYLONG	DAYCHG	BTICHGT	BTISF	BTISOG
DAYLONG	1.00				
DAYCHG	-0.99	1.00			
BTICHGT	-0.11	0.06	1.00		
BTISF	-0.11	0.14	-0.12	1.00	
BTISOG	-0.27	0.25	0.29	0.28	1.00
BTLCHGT	-0.13	0.16	0.08	-0.03	0.14
BVRCHGT	-0.04	-0.00	0.22	-0.31	0.02
CCTPPT	0.06	-0.08	0.00	0.08	-0.05
CLKSOG	-0.51	0.46	0.27	0.06	0.75
KKKCHGT	0.00	-0.05	0.55	-0.14	0.24

	BTLCHGT	BVRCHGT	CCTPPT	CLKSOG	KKKCHGT
BTLCHGT	1.00				
BVRCHGT	-0.15	1.00			
CCTPPT	0.18	0.04	1.00		
CLKSOG	0.18	0.14	0.00	1.00	
KKKCHGT	0.15	0.26	-0.13	0.26	1.00

Table 24. Pearson correlation matrix for variables in models for April.

	BTICHGT	BTIMAXT	BTISF	BTISOG	BTLPPT
BTICHGT	1.00				
BTIMAXT	0.09	1.00			
BTISF	-0.22	0.02	1.00		
BTISOG	0.05	-0.17	0.17	1.00	
BTLPPT	-0.12	0.14	0.14	0.03	1.00
BVRPPT	-0.10	-0.06	-0.02	0.02	-0.06
CCTMAXT	0.03	0.78	-0.01	0.16	0.12
CLKPPT	-0.15	-0.04	0.37	0.16	0.08
DAWPPT	-0.01	-0.17	-0.06	0.12	-0.07
DAYLONG	0.10	0.70	0.05	-0.01	0.05
FYKPPT	-0.15	0.03	0.81	0.15	-0.03
FYKSOG	0.07	-0.59	0.10	-0.19	-0.15
NTWMINT	-0.19	0.41	0.15	0.39	0.08
NTWPPT	-0.19	-0.01	0.06	0.03	-0.03
UMTCHGT	0.59	0.24	-0.01	-0.12	-0.09

	BVRPPT	CCTMAXT	CLKPPT	DAWPPT	DAYLONG
BVRPPT	1.00				
CCTMAXT	-0.03	1.00			
CLKPPT	-0.06	-0.04	1.00		
DAWPPT	0.04	-0.14	-0.07	1.00	
DAYLONG	0.00	0.73	-0.07	-0.13	1.00
FYKPPT	-0.03	-0.03	0.15	-0.03	-0.02
FYKSOG	0.11	-0.72	0.02	0.12	-0.56
NTWMINT	0.12	0.68	0.05	0.13	0.58
NTWPPT	0.28	0.04	-0.00	0.14	0.15
UMTCHGT	-0.10	0.04	-0.08	-0.07	0.20

Table 24. (continued)

	FYKPPT	FYKSOG	NTWMINT	NTWPPT	UMTCHGT
FYKPPT	1.00				
FYKSOG	0.10	1.00			
NTWMINT	0.11	-0.55	1.00		
NTWPPT	-0.04	-0.18	0.18	1.00	
UMTCHGT	0.06	-0.02	-0.16	-0.14	1.00

Table 25. Pearson correlation matrix of variables in models for May.

	BTIMINT	BTIPPT	BTLPPT	BTLSOG	BTLSF
BTIMINT	1.00				
BTIPPT	-0.01	1.00			
BTLPPT	0.12	-0.09	1.00		
BTLSOG	-0.19	0.02	-0.05	1.00	
BTLSF	-0.15	-0.03	0.28	0.14	1.00
BVRAVGT	0.42	0.01	0.09	-0.34	-0.11
CLKPPT	0.22	0.06	0.03	-0.07	-0.04
CLKSF	-0.16	0.39	-0.05	0.02	-0.02
CLKSOG	-0.53	-0.06	-0.09	0.61	0.12
DAWPPT	0.16	-0.10	0.02	-0.09	-0.06
DAWSF	-0.27	-0.03	-0.05	-0.04	-0.02
DAYCHG	0.52	0.02	-0.03	-0.23	-0.07
FYKPPT	0.14	-0.02	-0.06	-0.07	-0.03
KKKCHGT	-0.28	-0.14	-0.15	0.02	0.07
KPKAVGT	0.91	-0.05	0.06	-0.19	-0.16
NTWAVGT	0.48	0.00	0.08	-0.37	-0.20
NTWPPT	0.28	-0.10	0.12	-0.10	-0.04
OLCMINT	0.81	0.06	0.15	-0.07	-0.11
OLCPPT	0.09	-0.01	-0.02	0.01	-0.02
UMTSOG	-0.62	-0.08	-0.15	0.41	0.06

	BVRAVGT	CLKPPT	CLKSF	CLKSOG	DAWPPT
BVRAVGT	1.00				
CLKPPT	0.11	1.00			
CLKSF	-0.15	0.27	1.00		
CLKSOG	-0.61	-0.13	-0.02	1.00	
DAWPPT	0.12	-0.07	-0.06	-0.13	1.00
DAWSF	-0.11	-0.04	-0.02	0.15	0.23
DAYCHG	0.43	-0.02	-0.04	-0.47	0.16
FYKPPT	0.18	-0.04	-0.01	-0.12	0.13
KKKCHGT	-0.14	-0.13	-0.04	0.13	-0.11
KPKAVGT	0.39	0.24	-0.15	-0.50	0.20
NTWAVGT	0.90	0.14	-0.15	-0.64	0.09

Table 25. (continued)

	BVRAVGT	CLKPPT	CLKSF	CLKSOG	DAWPPT
NTWPPT	0.08	-0.09	-0.06	-0.14	0.19
OLCMINT	0.42	0.24	-0.03	-0.41	0.12
OLCPPT	0.10	-0.03	0.05	0.03	0.58
UMTSOG	-0.64	-0.22	0.17	0.51	-0.09

	DAWSF	DAYCHG	FYKPPT	KKKCHGT	KPKAVGT
DAWSF	1.00				
DAYCHG	-0.08	1.00			
FYKPPT	-0.03	0.16	1.00		
KKKCHGT	-0.06	-0.06	-0.16	1.00	
KPKAVGT	-0.25	0.60	0.11	-0.16	1.00
NTWAVGT	-0.14	0.43	0.17	-0.13	0.47
NTWPPT	-0.03	0.29	0.03	-0.13	0.32
OLCMINT	-0.26	0.33	0.14	-0.35	0.70
OLCPPT	-0.03	0.16	0.09	-0.11	0.09
UMTSOG	0.14	-0.41	-0.16	0.23	-0.54

	NTWAVGT	NTWPPT	OLCMINT	OLCPPT	UMTSOG
NTWAVGT	1.00				
NTWPPT	0.08	1.00			
OLCMINT	0.43	0.21	1.00		
OLCPPT	0.03	-0.00	0.07	1.00	
UMTSOG	-0.65	-0.24	-0.59	-0.06	1.00

Appendix C

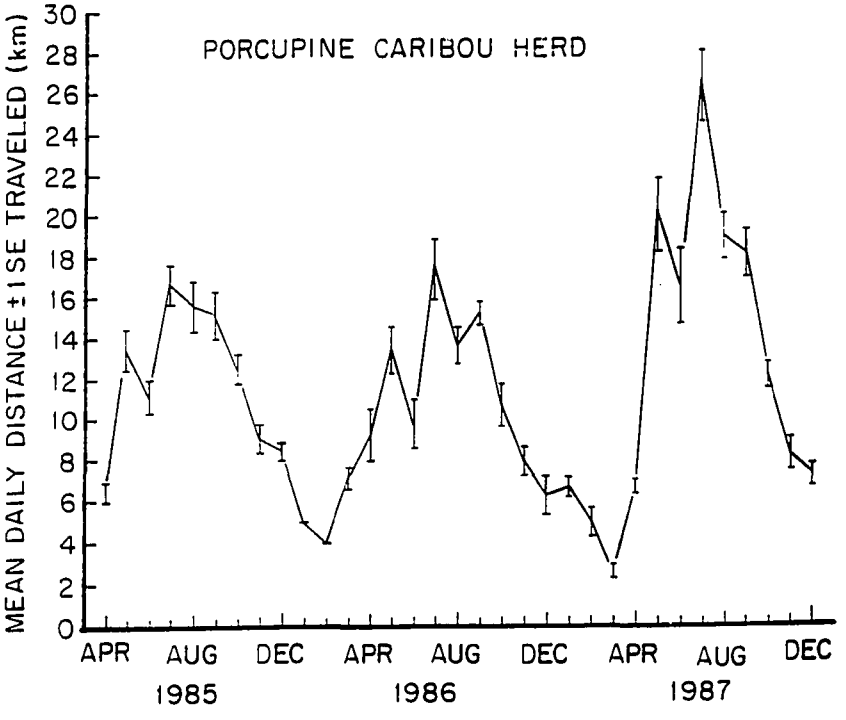

Figure 13. Rate of movement of the Porcupine Caribou Herd (from Whitten and Fancy 1990).

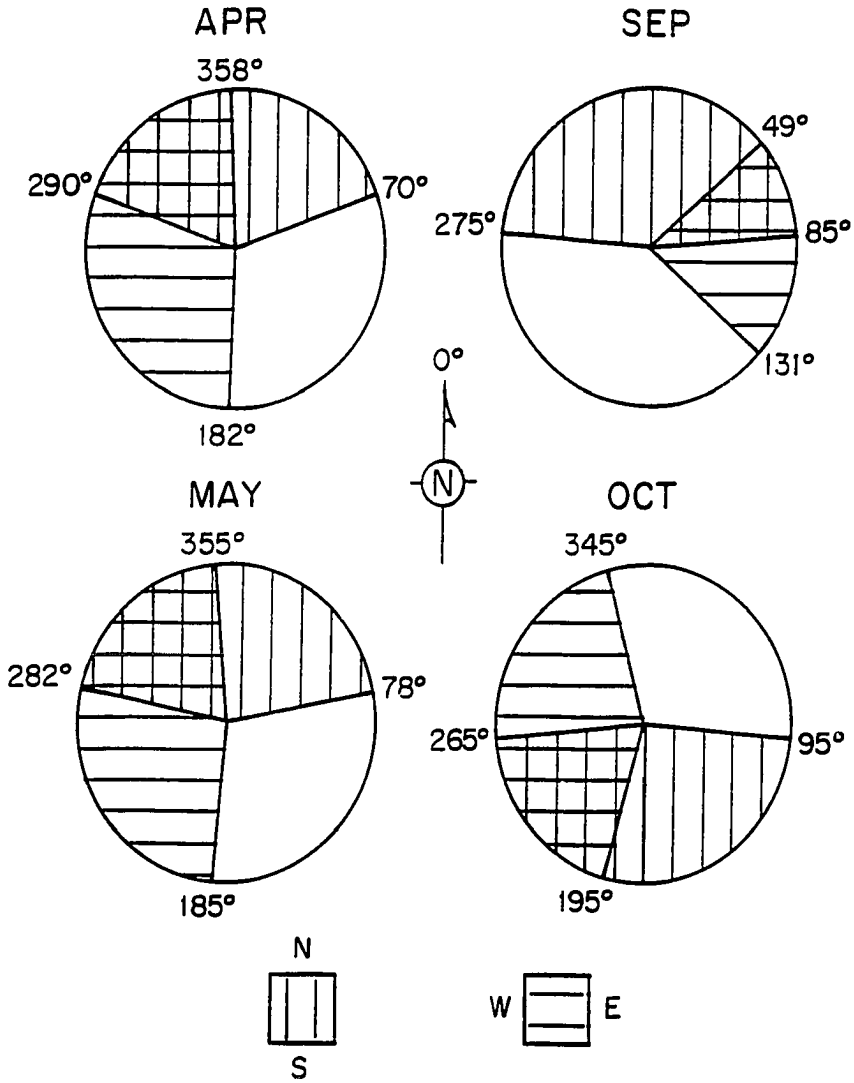

Figure 14. Mean directional movements of the Porcupine Caribou Herd for April, May, September, and October.